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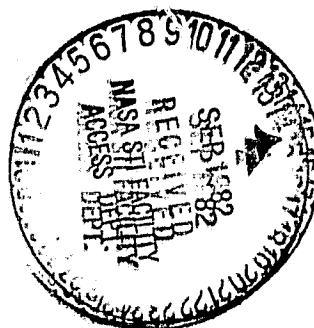
The Influence of Varied Gravito-Inertial Fields on the Cardiac
Response of Orb-Weaving Spiders

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Anniversary Report
August 1982

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Prologue

This anniversary report contains a detailed description of the methods and results of the work during 1981-82. Because it is important to document casual observations as well as technical methodology in gravitational experiments, the appendix is employed rather freely. The major findings are in the body of the report. Methods of procedure, instrumentation, mathematical formulae and other observations on spider behavior in the hyper-g field are given in appendices. The table of contents should be sufficient for the reader to identify the various portions of the report. Note that the introduction is the initial grant introduction.

To all who examine this report; should you wish to communicate on any aspect of the work I would be happy to do so.

This work on the gravitational physiology of the spider began with the observations that 1. they orient with respect to G, 2. orb-webs are constructed with respect to the G vector and 3. silk spinning and the physics of silk is adjusted according to body weight (a consequence of gravity). The scientific literature is devoid of direct attempts to study the arachnid sense of gravity. Perhaps with the recent growing interest in the field of Gravitational Physiology this will be rectified. Our present knowledge describes an animal which appears to have a very low absolute threshold for G and a substantial dynamic range of response. We can say with some confidence that the species Araneus sericatus can discriminate Gz intensities on the order of 1.001 or less and 2Gz. If this is the case the perception of gravity by the spider might rank just under the dynamic range of the exquisite senses of hearing (ca 8 log units in man) and vision (ca 12 log units in man). Our present research attacks the issue of how spiders extract this information from the gravitational

environment.

Abstract of Anniversary Report

The Gz transfer function has been described for the orb-weaving spider A. sericatus. The functional relationship between the heartrate and the intensity of G is linear in the form of:

$$Y = a \log Gz - 1 + k$$

The heartrate in unrestrained animals was recorded by a laser plethysmograph developed specifically for this purpose. Following a control sample heartrates were taken post-rotation between 1.001 and 1.5 Gz in 6 steps. The underlying distribution of heartrates does not appear significantly different from a Gaussian distribution.

A method of varnishing the legs of the spider has been developed. This was done in order to compromise the lyriform organs, especially those located on the patellae. The lyriform organ is hypothesized to serve the receptor role in the transduction of gravity related stimuli. In preliminary animals the Gz function, post varnishing of the patellae, appears to be changed in the direction of poorer discrimination. We have also observed that the resting heartrate following the varnish procedure is substantially increased. This tachycardia is statistically significant.

The spider response to hyper-G is consistent with published observations on the mechanics of the lyriform organ. Thus, further evidence for the lyriform hypothesis is offered.

Future work includes 1. a systematic examination of the role exoskeletal sense organs (the lyriform) play in Gz sensitivity. 2. an evaluation of tilt 3. determination of the amplitude density function of the heartpulse and 4. extension of Gz stimulation to intensities lower than 1.001 and higher

than 1.5.

Method for determining the gravity transfer function in the spider.

Our procedure employed the cardiac rate as an indicator of response sensitivity to various levels of Gz. Gz, produced by centrifugation varied between 1.001 and 1.5. An ascending series of intensities was used because we could not be certain that experience at the higher Gz levels might not exert too great an influence on experience at lower levels within an experimental session.

Preliminary work suggested that the dynamic range of the response to Gz might be quite large. Therefore the experimental design employed more than one log unit of the Gz intensity range. In order to assess as much of the range as possible a 1, 2, 5 series was used. The Gz values were as follows 1.001, 1.002, 1.005, 1.01, 1.02, 1.05, 1.1, 1.2 and 1.5 Gz.

An attempt was made to expose each animal to each level for ten minutes during a single experimental session.

The procedure was as follows:

A spider was selected from the colony if it was in a dorsal-up orientation. This insured that the legs were on the substrate of the culture dish (its home cage). The culture dish was gently carried to the centrifuge, placed in a secure holder on the gimbal and the laser unit was swung into position over the abdomen. The laser was adjusted in x and y movement by a set of micromanipulators. The laser beam was directed to the abdomen just above the heart. We avoided shining the light on to the spiders eighth eyes which are located on the cephalothorax. Figure 1 page 6 is a photograph of A. sericatus. A circle on the abdomen indicates the best region for obtaining the cardiac pulse. Following a few adjustments of the laser a strong, clean beat can be obtained in a few seconds. Keeping in mind that the laser light

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penetrates the abdomen and a photocell is located directly beneath the culture dish very large animals or animals with exceptionally dense abdominal pigmentation may make recording difficult. But even in these animals it was usually possible to find a good spot to transilluminate.

The laboratory was darkened and following a rest period of ten minutes a sample of 100 heartbeats was recorded. Following this rest-control sample the laser was swung away from the centrifuge and the animal presented the lowest Gz intensity for 10 minutes. The choice of a 10 minute exposure time was based on preliminary observations which indicated that the post-rotatory response did not recover for at least 10 minutes following a 10 minute exposure.

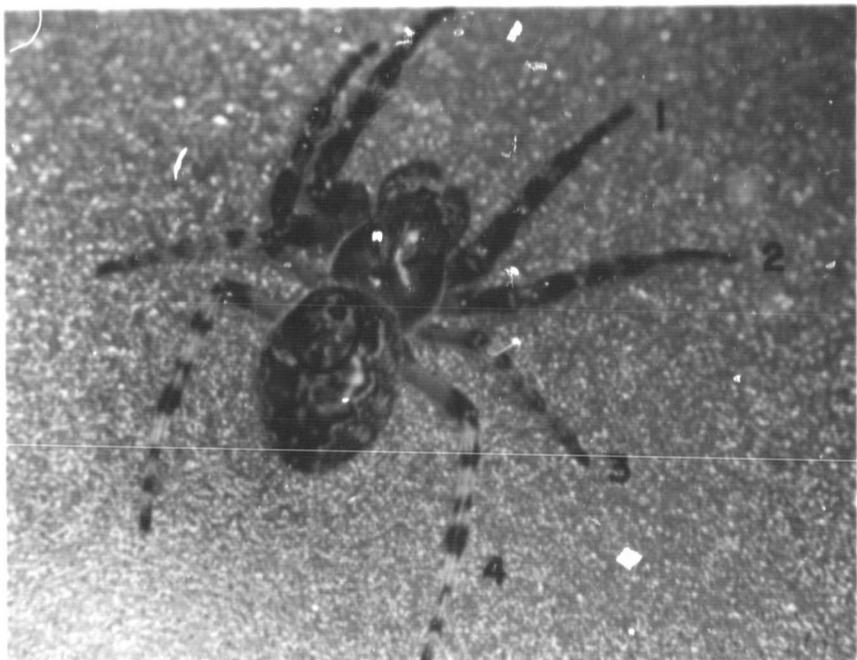
When the Gz exposure was completed the centrifuge was slowly brought to a stop (over a period of 60 seconds) in front of the laser, the laser was swung back to the same locus on the abdomen and a sample of 100 beats taken. When, in a few instances the animal had moved it was either returned to the colony or given a long rest period and relocated under the laser light once again..

The treatments within a recording session was: rest--1.001 Gz--rest--1.002 Gz--rest--1.005 Gz etc. to 1.5 Gz.

Total running time for an experimental session was more than 190 minutes. Taking into account apparatus adjustments and so forth the work was typically limited to one animal per day.

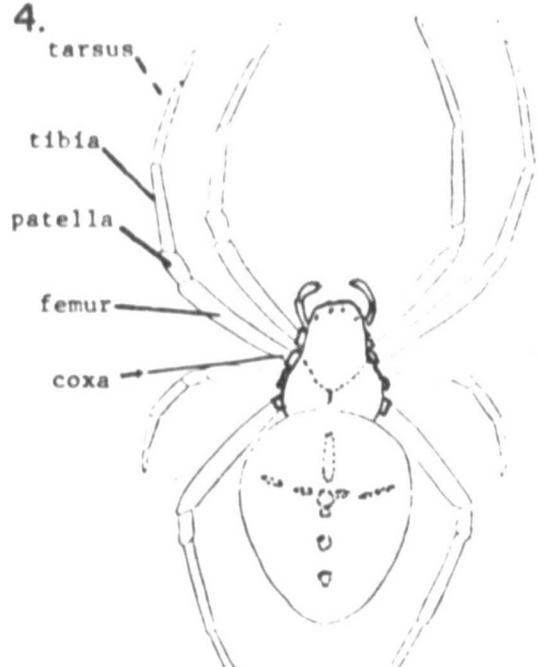
The animal was returned to the colony after the experiment. Casual observations of the spiders indicated no untoward effects in their eating, drinking or general behavior following centrifugation. Spiders are quite sedentary and they appeared as inactive after rotation as before rotation.

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ARANEUS SERICATUS.
THE CIRCLE INDICATES OPTIMUM LOCUS
OF LASER BEAM ON THE ABDOMEN.
THE LEGS ARE NUMBERED 1,2,3 AND 4.
(ca 6X)

Fig. 1



RESULTS

Figure 2 shows time interval histograms of the spider heartbeat photographed from the computer display. The histograms result from 100 successive heartbeats taken at rest (control) and post 1.001, 1.002 and 1.005 Gz. The Gz intensities are the lowest of our series given to the animal. The abscissa shows the inter-beat interval in seconds and the conversion to BPM. The conversion formulae is:

$$\text{BPM} = 1/\text{interval (secs)} \times 60$$

The mode (peak) of the control rate is near 2.5 secs (ca 24 BPM). After 1.001 Gz experience the mode has shifted to about 2.8 seconds (21 BPM). The distributions shift to the left (higher heartrates) with increased Gz. The increased spread of the 1.005 histogram is produced by a few short and a few extended inter-beat intervals. We have been employing the median as the measure of central tendency. With the advent of a computing system the mean and variance can be efficiently calculated.

Figure 3 shows the mean heartrate for a group of animals as a function of log Gz. Seventeen animals contributed to the results between 1.001 and 1.2 Gz. Association with each mean data point is a representation of the standard deviation (σ). The data points were best fit with a regression line in the form of: $Y = a \log Gz - b + k$. The regression curve is the predicted Y values. The goodness of fit indicates that 92 percent of the variance can be accounted for by the logarithmic regression line ($R^2 = .92$).

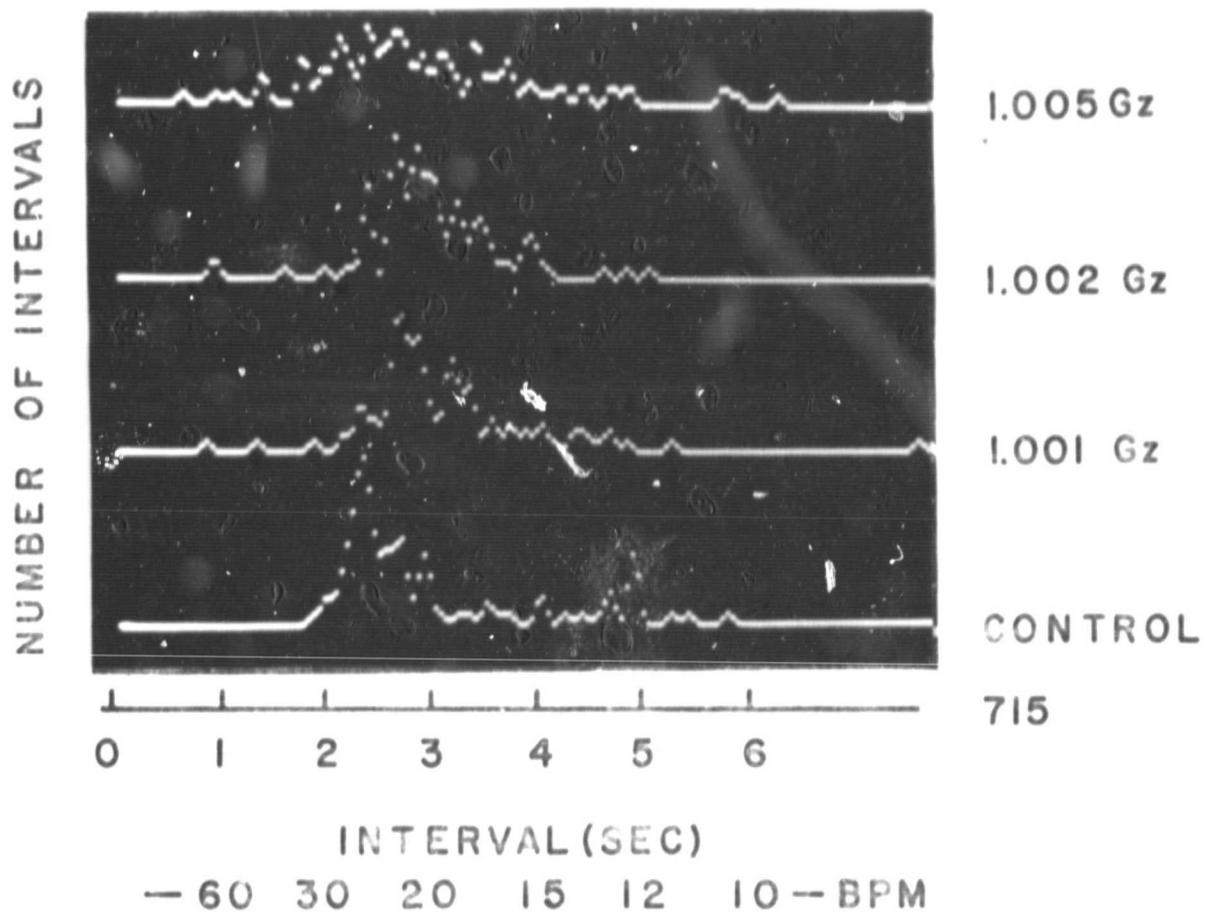


Fig. 2

TIME INTERVAL DISTRIBUTIONS OF THE HEARTBEAT
OF THE UNRESTRAINED SPIDER. EACH HISTOGRAM
CONTAINS 100 BEATS POST ROTATION. Gz EXPOSURE
TIME = 10 MINUTES.

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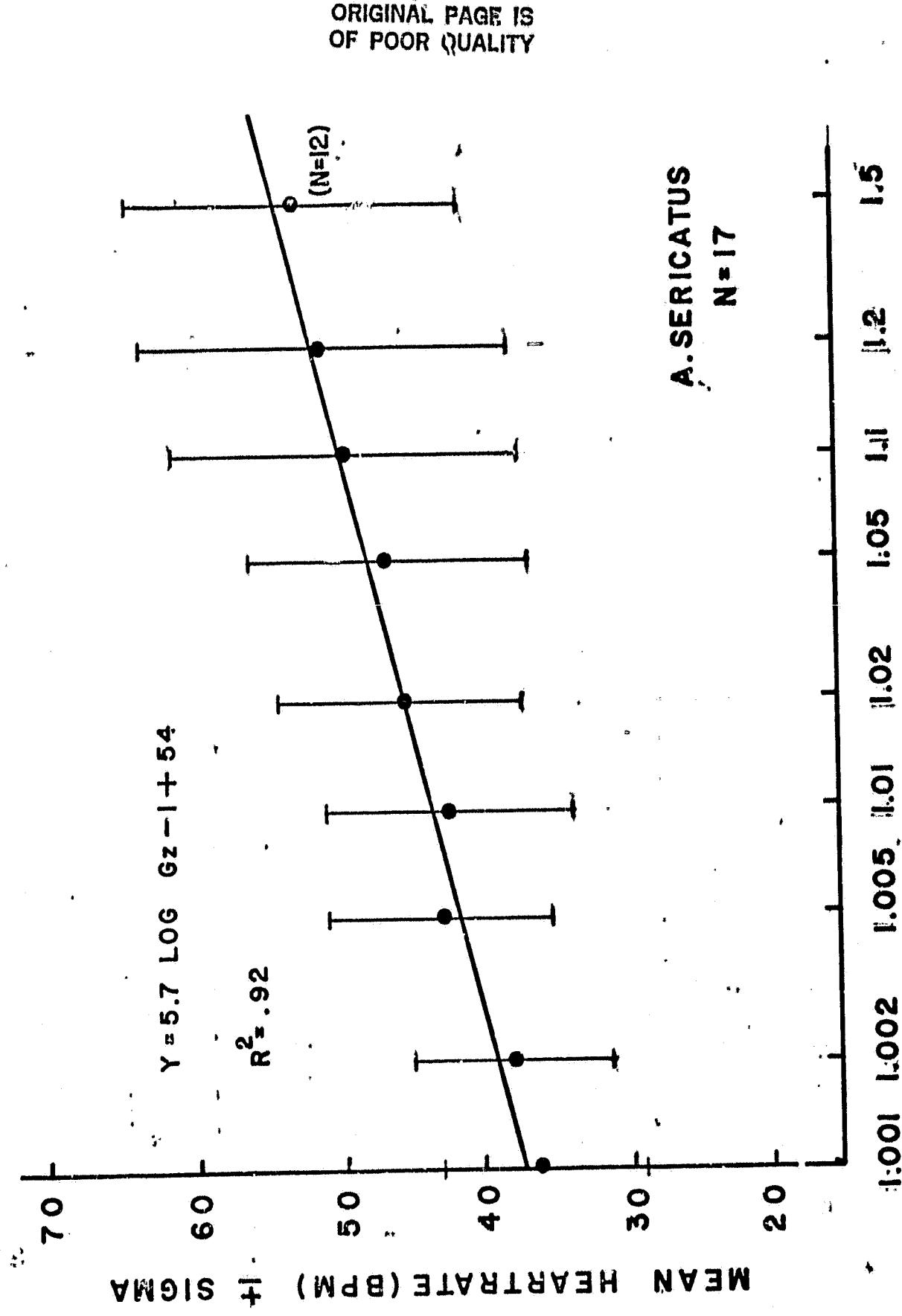


Fig. 3

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Figure 4 page 12. Represents the linear fit for 12 spiders exposed to 1.001 through 1.5 Gz. The abscissa is log Gz and the ordinate is the y' (predicted rate) based on the logarithmic regression calculated separately for each animal. The equation is in the form of:

$$y' = a \log Gz - 1 + k$$

y' = predicted rate

a = slope

k = intercept

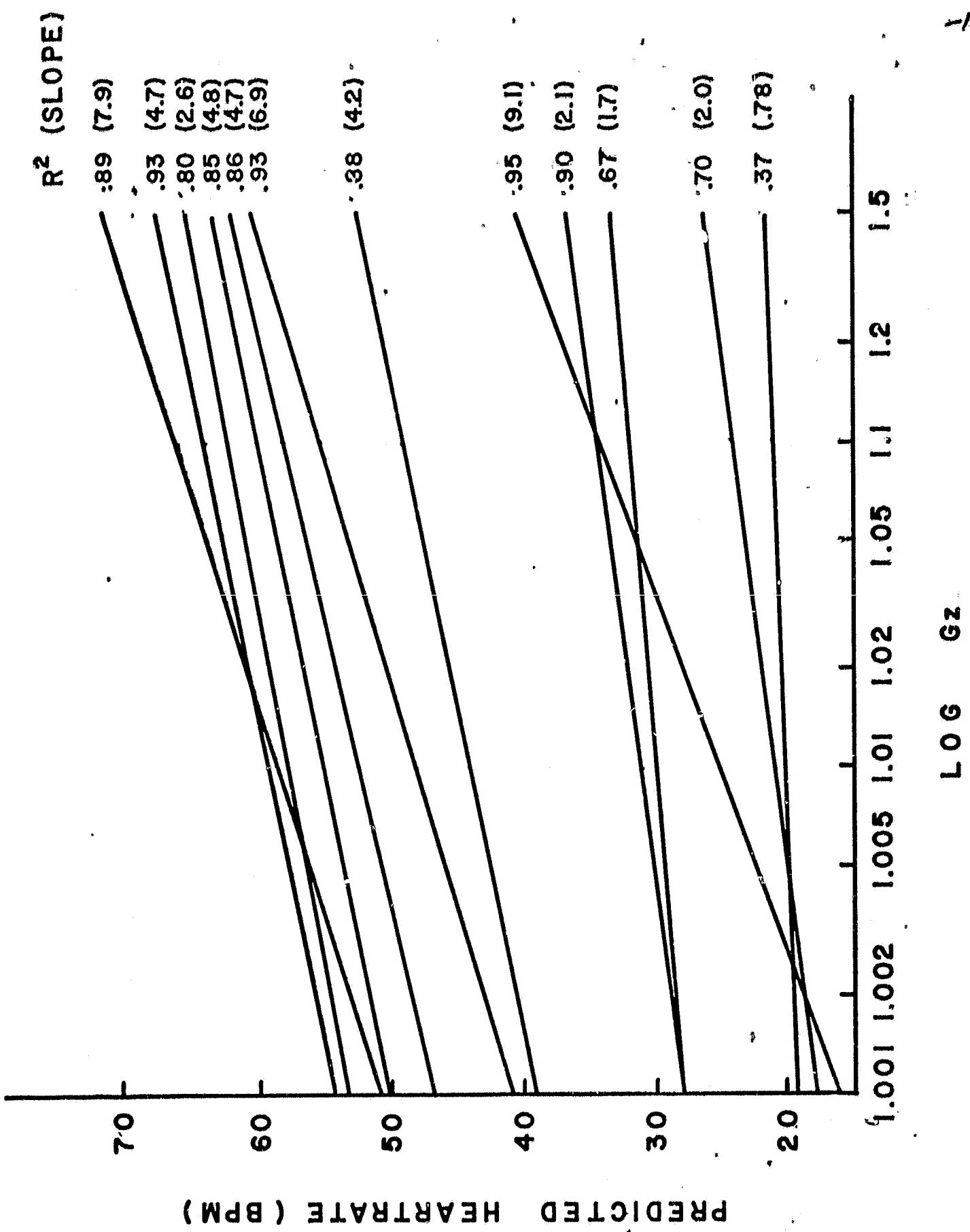
R^2 in the figure shows the goodness of fit obtained for each animal. The slope is indicated in the adjacent column. R square (the square of the correlation coefficient) is sometimes called the coefficient of determination. When multiplied by 100 it gives us the percentage of the variance in Y that is associated with or determined by variance in X. Another way to consider R^2 is in terms of the percentage reduction in errors of prediction of Y from X. For example: $R^2 = .37$ and $R = .61$ error reduction = 20%

$R^2 = .95$ and $R = .97$ error reduction = 70% (see Guilford, 1950 page 409 for an interesting analysis of goodness of fit).

In the "worst case" a spider function with a .37 R^2 and slope of .78 errors of prediction are reduced by 20 percent. More than one half the variance is accounted for by those regression curves with R^2 greater than .70 ($R = .84$). This allows us to conclude that a log function is a good predictor of the cardiac behavior in response to the various Gz intensities. The figure also shows that differences among them in terms of the rate of the beat are substantial...ranging from less than 20 to more than 50 BPM at 1.001 Gz. This is not surprising nor particularly disturbing when we recall that the neurogenic heart of the spider can be modulated by external (sensory) as well as internal

stimuli.

The mean resting heart rate for the animals contributing to the curve in Figure 3 is 42 ± 10 BPM ($N = 17$). The mean resting rate calculated from a larger sample (preliminary and the above animals) yield an estimate of 34 ± 12 BPM ($N = 54$). Clearly spiders demonstrate substantial individual differences in the basic resting rate. We have observed (and reported this earlier) that very low radial acceleration will elicit a bradycardia in certain individuals. We are not prepared at this time to undertake a thorough analysis of this phenomenon. The data are available on magnetic tape and await the development of our future computer analyses. It should be noted that during the early stages of the research when animals were restrained the bradycardia associated with slow rotation was frequently observed. Hopefully an explanation will be forthcoming.



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Preliminary Results of the Varnishing Experiments

The "removal" experiment is commonly employed by neuro-physiologists and physiological psychologists. In experiments with animals it is possible to remove systematically parts of the brain or to destroy, or compromise tissue selectively. The experimenter then observes the defects that result from the procedure. The logic of the manipulation is that the ablation or interference with a structure provides evidence for its role in normal behavior. This procedure is not without difficulties. Sometimes intervention may disrupt behavior only temporarily. Other mechanisms might be brought into play. Removal experiments must be done with great care for them to be interpretable. The removal experiment will not divulge the properties of the structure under study, it can provide insight into its importance.

We have developed a procedure for compromising the exoskeletal sense organs by varnishing. As expected there were several cul-de-sacs mostly associated with determining a varnish which would flow easily, attach to the waxy exoskeleton of the spider and would not be harmful to the animal.

It might be useful for the reader to be aware of the substances discarded. A dental acrylic resin was tried (Jet Acrylic) however the acrylic beads are very large and may not flow into the lyriform organs (our hypothesized G receptors). Further during the curing process acrylic develops heat. Sobo fabric glue (a water-based substance) would not adhere to the cuticle. Insl-x is a tool-dip which, in small portions, dries very quickly. We employ it in the lab for insulating tungsten microelectrodes. It adheres beautifully to the spider cuticle and dries hard in perhaps a minute. Insl-x is toluene based. The minute amount employed does not appear to harm the animal when applied to the exoskeleton. In order to see the clear varnish and to photograph it, a

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small amount of sudan black was added to a varnish sample. Figure 5 (page 16) is a photograph of the patallae of a spider varnished with Insl-x. Working with a Zeiss operating microscope and employing a single tungsten wire as a brush the entire leg or any portion of it can be varnished...with a little experience. The areas corresponding to the joints are, of course, avoided. During the varnishing procedure the animal is anesthetized with CO_2 . The CO_2 flow rate is at 0.1 cu. ft/hour. The animal recovers quickly after the gas is removed. We can show that light CO_2 anesthesia has no observable effect on the spiders subsequent eating behavior nor on its web building behavior.

Several animals on which 6 to 9 Gz data points were obtained have been submitted to the varnishing procedure. The results of our observations are given in Figures 6 and 7 page 17. The ordinates are median heartrate in BPM and the abscissac are given in log Gz. Curves marked "normal" describe the Gz function prior to manipulation of the animal. Curves labeled "Patallae legs right and left 2" describe the Gz function several days after varnish procedure. The patella of the spider leg can be identified by the reader in Figure 1 page 6. Animal 715 was given two procedures. First the patallae were varnished and a Gz record taken, then, several days later the patallae and the tibia on all 8 legs were varnished and the Gz stimulation repeated.

The "normal" curves are representative of the functional relationship between heartrate and G. It appears that the function obtained following varnishing the patallae on the set of front legs (all four) results in a curve with little slope and, in the case of spider 64, with a decrease in heartrate with increased Gz. One could conclude from the initial observations that varnishing the patallae modified the Gz sensitivity function.

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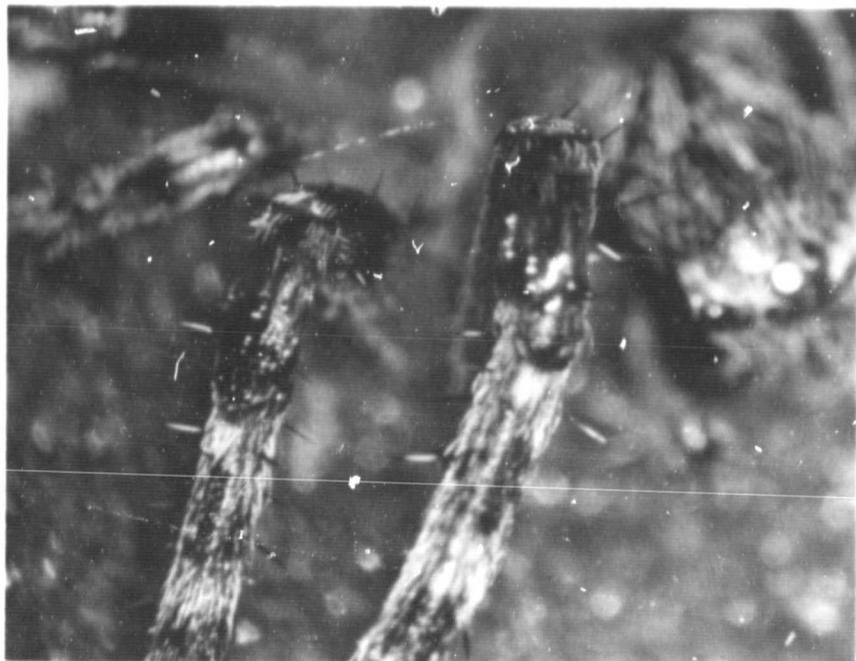
The results shown here and those from 3 other spiders (from which Gz functions were not taken at the time of the writing) present a curious phenomenon. The heartrate, post-patellar varnishing is increased. This occurs with respect to Gz stimulation and can be observed in the resting-control rates.

Table 1 page 14 is an analysis of the resting/control rates for 6 animals before and after varnish was applied to the patellae of legs 1 and 2, left and right sides.

All spiders showed an increase (difference column) post varnishing. The average rate is 47.5 BPM before and 67.2 BPM post varnish. This is a relative increase of +41.5 percent. Table 1 also shows the result of a non-parametric statistical test on these data which is statistically significant beyond the .05 level of confidence.

In a second procedure spider 715 had the petellae and tibiae on all eight legs varnished. The resulting Gz function appears rather flat up to 1.02 Gz followed by a large rate increase at 1.05 Gz and beyond. This procedure will be repeated on other animals to assess the reliability of this single observation.

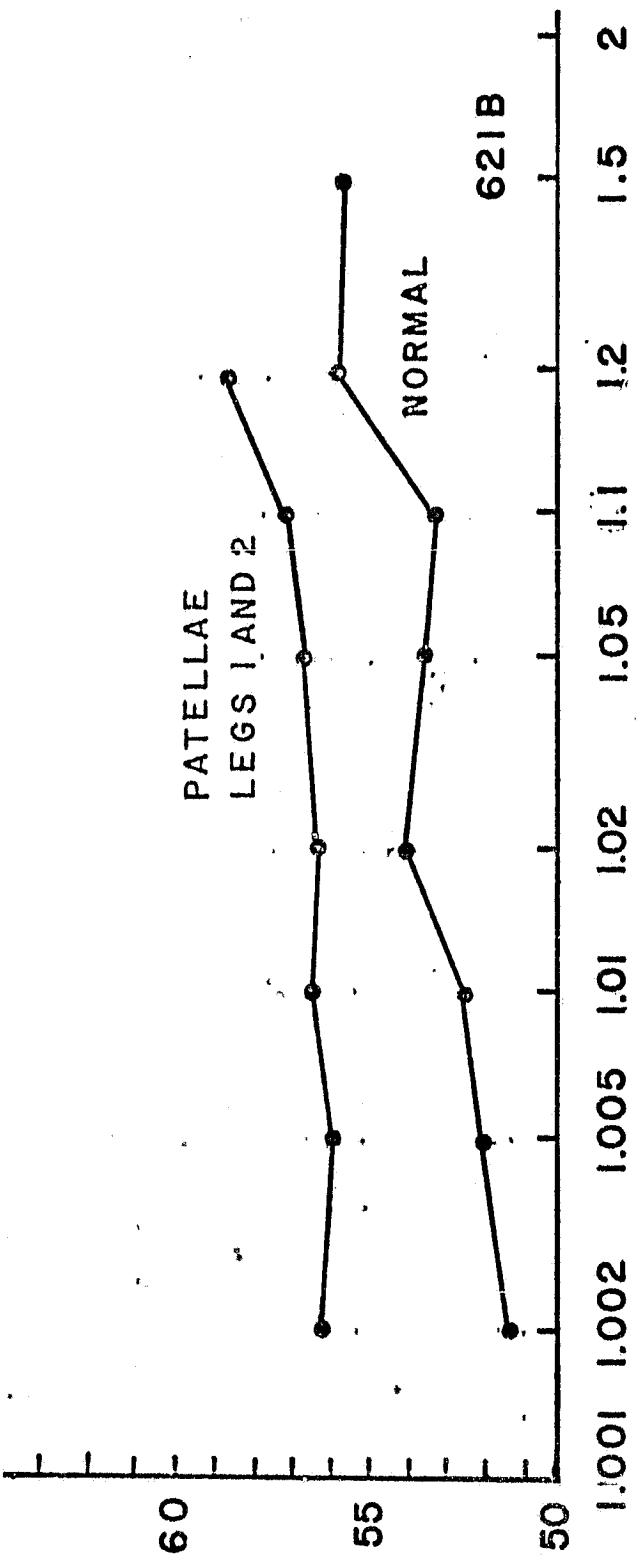
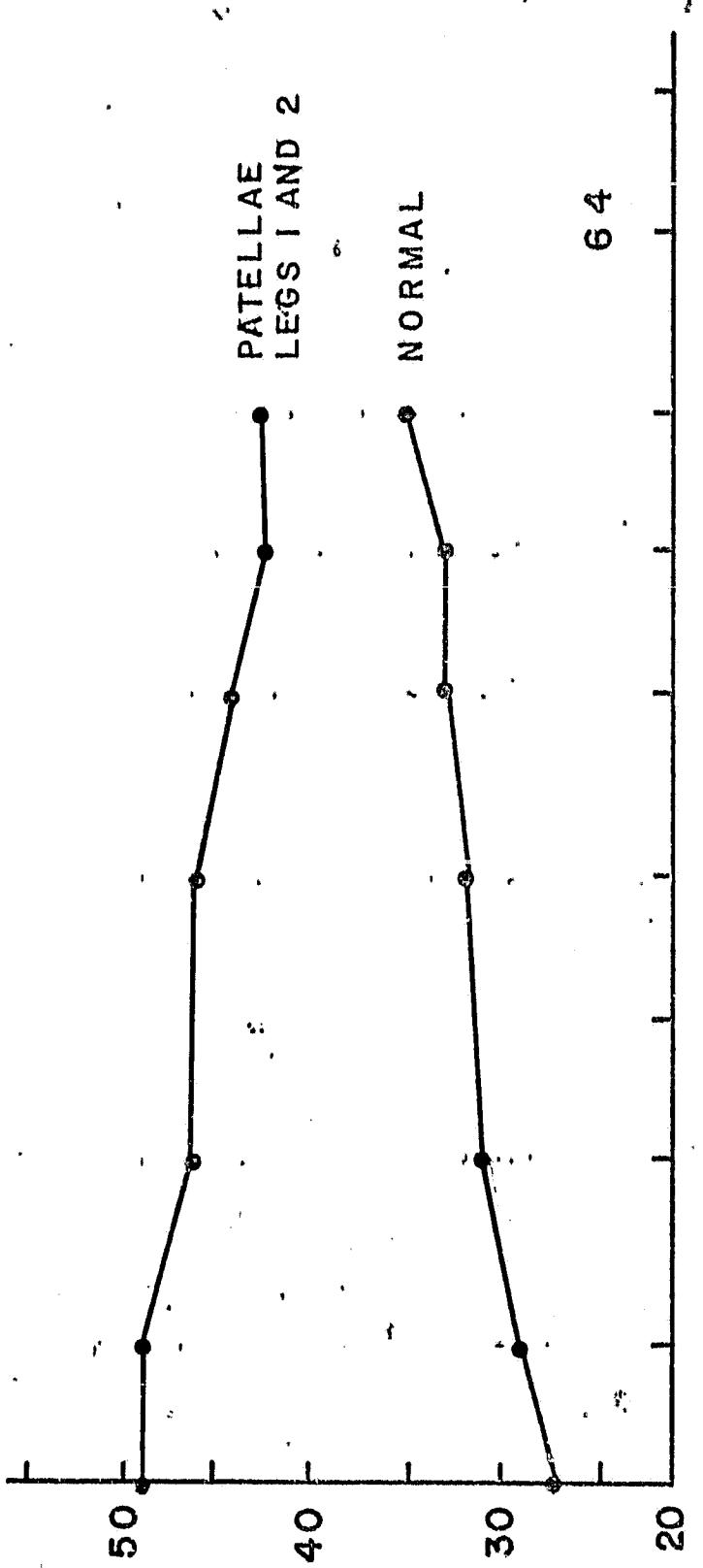
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RIGHT LEGS, I AND 2, OF A. SERICATUS.
PATELLAE VARNISHED WITH INSLX.
(ca 25X)

Fig. 5

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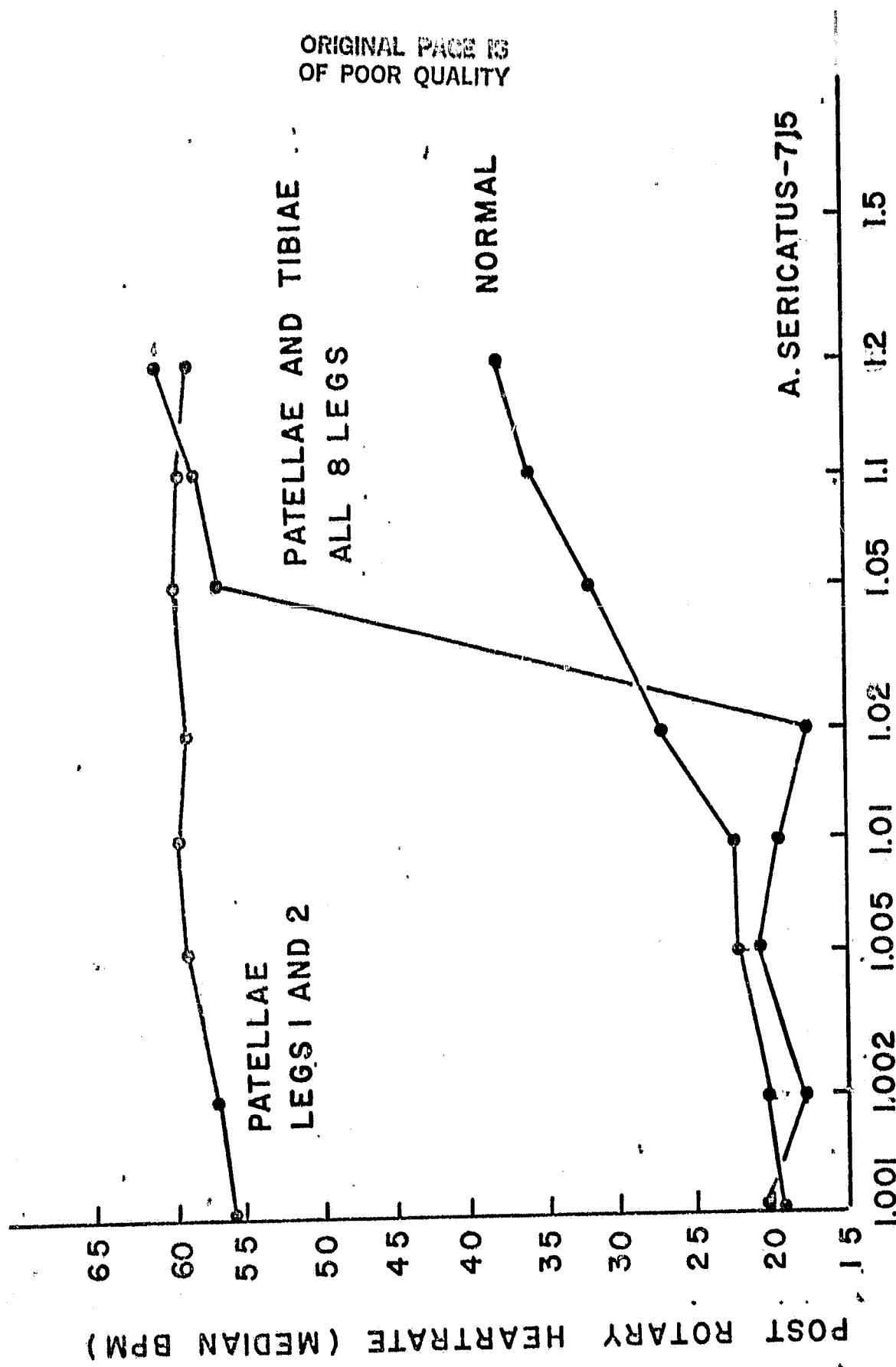


Fig. 7

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Table 1. Analysis of resting heartrates (BPM) for 6 spiders before and after (+ 2 days) varnishing the patellae of legs 1 and 2 , right and left.

BEFORE	AFTER	DIFFERENCE	SIGNED-RANK
57	82	+25	+5
49	59	+10	+2
68	88	+20	+4
30	52	+12	+3
55	63	+8	+1
26	59	+33	+6

Mn 47.5 Mn 67.2

The relative increase is +41.5 percent

The Wilcoxon Matched-Pairs Signed Ranks Test (Siegel 1956)

Sum of + ranks = 21

Sum of - ranks = 0

T = smaller sum of like-signed ranks = 0

From a Table of Critical Values of T for N=6 and T=0 the null hypothesis is rejected at the .05 level of confidence. (note: this test has $3/\pi$, 95 percent of the efficiency of a parametric t test for small samples)

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Discussion and Conclusions

Observations on the Logarithmic Law and the Spider Transfer Function

Fechner (1860) proposed that the differential threshold (DL, just noticeable difference) could be employed as a standard unit to measure the magnitude of sensation. According to Fechner, the relationship between the sensation (response) continuum and the stimulus intensity continuum was such that equal stimulus ratios corresponded to equal increments of sensory response. Under the assumption that all differential thresholds (DL) within a modality were equal (not a good assumption) it follows that as the number of DLs grow arithmetically the stimulus intensity increases geometrically. That is, relatively larger and larger outputs in stimulus energy are required to obtain corresponding sensory effects. The arithmetic to geometric progression reduces mathematically to a logarithmic relation:

$$S = k \log I$$

This states that the magnitude of sensation (S) is proportional to the logarithm of the physical intensity of the stimulus (I).

Stevens (1961) contended that the relationship between stimulus magnitude and sensory magnitude is not logarithmic but rather a power law. According to a power law, sensory magnitude grows in proportion to the physical intensity of the stimulus raised to a power: $S = kI^b$ where b is an exponent that is constant for a particular sensory dimension (or modality) and set of experimental conditions. In logarithmic form the power law reduces to: $\log S = b \log I + \log k$. This function tells us that equal stimulus ratios produce equal sensory ratios.

Both laws were invented to express the relationship between stimuli and the sensational (psychologically experienced subjective) aspects of the sensory

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scale. It is generally agreed that for many psychological tasks the power law is a better representative of the relationship between stimuli and sensory experience. In the physiological literature roughly logarithmic transfer functions are found between stimulus intensities and variables like neural firing rates. This is a corroboration of the Fechner Law. MacKay (1970) observes that, "...many pitfalls beset the would-be-integrator of psychological and physiological data". There is hope in obtaining a rapprochement..perhaps the difference is at the level of analysis.

We human beings do not easily empathize with spiders and we can never know what the animal experiences when angular acceleration is manipulated. We can however compare some of our present results with experiments in other species and perhaps obtain a kind of "feeling" and perspective of the data.

Peters (1969) provided a compilation of studies (some old) which indicate the absolute threshold to linear acceleration in man to be between .006 and .027 Gz. These values depend upon the method used and the position of the subject. Radial acceleration thresholds in man were reported by Walsh (1961). He used perceptual criteria. His values were on the order of .0019 and .0025 Gz (depending on the direction and the position of the subject). Our present results show that the spiders, as a group, respond to at least .001 Gz + 1 G. If the curve (Figure 3) were to be extrapolated to some lower limit the absolute threshold might be in the region of .0005 Gz. It appears that the orb-weaver is as sensitive as the human to changes produced by increases in gravito-inertial stimuli.

Gaultierotte and Gerathewohl (1965) recorded single otolithic units from a frog during a Keplerian flight path. Their records show that changes in Gz between 0.0 and 0.56 were logarithmically related to the frequency of unit

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discharge. In an experiment more comparable to our spider work (a physiological response was employed to assess Gz sensitivity) Miller and Graybiel (1965) studied ocular counterrolling (humans) during a Keplerian trajectory. Their results indicate that above approximately 0.6 Gz relative otolith activity becomes proportional to the G force according to a logarithmic law.

The results of the spider experiments are comparable with results taken on other animals, and where other methods have been used. We do not presently have data above 1.5 Gz that we wish to report. There is a likelihood that the linear (log) portion of the function extends beyond 2 Gz. In terms of the extrapolated upper limit of the transfer function the spider might respond over a 5 log unit range above threshold. In comparison with the exquisite senses of vision and hearing, which operate over a range of about 12 to 8 log units, respectively, the spider G function is perhaps more constricted but, still impressive.

The Absolute Sensitivity of the Spider to Gz

The general Pauplan of the lyriform organ is such that deformation by very small forces becomes possible. We have indicated earlier that several studies which assessed the displacement sensitivity of the lyriforms indicate absolute thresholds much less than a micrometer (introduction in appendix). A response which is directly relevant to our Gz sensitivity experiment is that of Barth (1981) who reported the angular displacement of the leg which would just evoke a unit discharge from a lyriform slit. For a threshold angle of .0006 degrees an organ on the tibia required a force of 40 micro Newtons (4×10^{-5} N).

Let's assume that an increment to the normal weight ($g = 1$) on the legs produces a sensory discharge and that this stimulus increment can be accomplished by: 1. moving the leg (as reported by Barth), 2. adding weight to the cephalothorax, or 3. producing a centripetal component to total G by centrifugation.

A few calculations (Appendix I) show that the vector sum of g_e (9.8 m/s/s) and a radial acceleration of 0.4 m/s/s results in a total acceleration of 9.814- m/s/s. The ratio of g_t to g_e is 1.0008 Gz. The contribution to the absolute weight value of the spider by the centripetal component is 40 micro N. Perhaps it is not coincidental that near the absolute threshold to Gz stimulation (circa 1.001 Gz) in the present research the force added by the radial component is 43 micro N. Assuming the correctness of this argument it becomes one of the rare but happy circumstances in which disparate behaviors (cardiac reflex vs unit discharge) with different species (orb weaver vs a hunting spider) and in different laboratories (Frankfurt vs Philadelphia) are correlated.

At present we do not know how the several lyriform organs on the several

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legs summate or contribute as a group input to the CNS of the spider. Clearly, the Gz threshold should be elevated as the lyriforms are systematically compromised. Further, the animal should become less discriminating of changes in Gz when fewer receptors input the CNS. The above argument also implies a scale factor in that very small, light animals (e.g., neonates) might show elevated Gz thresholds relative to a typical 100 mg animal.

Considerations on the spider heart and its' role in movement and orientation.

Parry and Brown (1959) observed a "resting pressure" of 5 cm Hg within the spider leg. They also observed a transient increase to 40 cm Hg or more associated with, or in preparation for movement. (Peak systolic pressure in human beings is often given as 120 mm Hg).

Wilson (1967) (appendix K) observed that there is no anatomical evidence for a mechanism which can generate pressures like these within the leg itself, nor could Parry and Brown account for a leg mechanism. The alternative explanation is that the heart can generate high pressures which are involved in the movement of the legs. The legs of spiders appear not to contain extensor muscles, consequently some kind of hydrostatic mechanism may be employed; 1. to regulate postural homeostasis and 2. to initiate and control movement. Changes in internal fluid pressure could also be involved in the mechanics of the liquid silk during spinning.

Wilson preferred not to implicate the heart in the generation of transient pressures of the cephalothorax. He argued that the musculi lateralis could produce pressure in the prosoma (cephalothorax) and the subcuticular muscle sheet in the opisthosoma (abdomen). Thus high transient pressures in the spider, according to the Wilson model, would be associated with a "twitch".

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This hypothesized twitch should be observable during recordings from the abdomen and it should precede changes in amplitude or rate of the cardiac response.

There appears to be little evidence for this in the present research. Spiders will periodically produce a kind of "whole body twitch". During extended recording of the heart (unrestrained animal) we can demonstrate a rapid burst of beats and sometimes a large amplitude increase but just prior to a motor response. During tilt and post tilt one can observe changes in the rate and often amplitude of the cardiac reflex which are not preceded by motor activity. Such observations add to the belief that the heart-pump is the mechanism which builds up hydrostatic pressure for the extension of the legs and the maintenance of orientation.

Perhaps the pedicel (tube connecting the cephalothorax to the abdomen) is restricting the venous return and produces high pressures in the cephalothorax? That would imply that the pressures in the cephalothorax remain at a rather constant high level, which seems not to be the case. The evidence for this is not "in yet". Wilson made an interesting point about the pedicel that it evolved as a kind of joint so that the abdomen and spinnerets may be maneuvered without affecting the balance of the spider. The abdomens of orb spiders are quite large because they have to carry voluminous silk glands. It has often been observed that they fatigue easily when forced to run. Perhaps they have difficulty pulling an unwieldy abdomen along a substrate (orb spiders usually hang passively in webs)? Perhaps there is an inefficiency in the respiratory system (the pump cannot keep the pressure up)? The latter hypothesis seems to be a simple explanation to me.

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Analyses Planned for the 1982-82 Period

We have often observed that the cardiac reflex of the spider in response to Gz changes its magnitude. Therefore we plan to examine the amplitude distributions before and after Gz stimulation. Our plan is to perform a pulse height analysis employing a computer. A tentative system has been designed which digitizes and distributes the relative magnitudes of the heartpulse. Figure 8 shows amplitude density functions (ADF) for the spider heart before and after exposure to $G_z = 1.1$. The post rotary amplitude is increased by about 17 percent relative to the control amplitude. There may also be some changes in the frequency of occurrence of smaller magnitude beats in the post-rotary function. Further analyses might expose this and other phenomenae associated with hyper-G stimulation.

Preliminary examination of the spider response to tilt has suggested that there is merit in evaluating this independent variable. Not only does the spider heartrate change when the animal is tilted but the amplitude of the pulse is increased. Figure 9 demonstrates this for a 30 degree tilt. One benefit of the tilt experiment is to permit continuous recording before-during and after the stimulus is presented. Our working hypothesis is that compromised lyriform organs will result in decreased sensitivity to tilt (perhaps in the domain of pulse amplitude as well as pulse rate).

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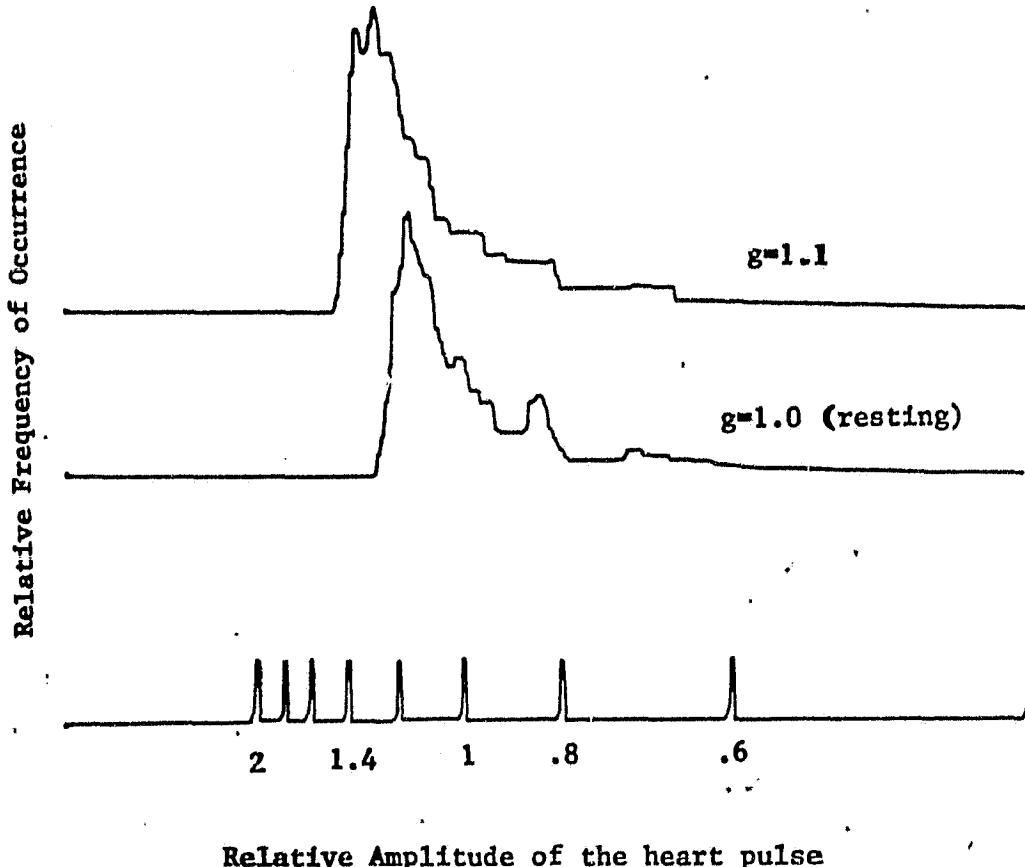


Fig. 8

THE AMPLITUDE DENSITY FUNCTION FOR TWO, THREE MINUTE CARDIAC SAMPLES BEFORE AND AFTER EXPOSURE TO $g = 1.1$. THE ORDINATE REPRESENTS THE PROPORTION OF THE TIME THE HEARTBEAT HAD AN AMPLITUDE AS LARGE AS THE VALUE SHOWN ON THE ABSCESSA. THE MODAL AMPLITUDE ON THE CURVE LABELLED $g = 1.1$ IS 17% GREATER THAN THE MODAL AMPLITUDE OF THE RESTING FUNCTION.

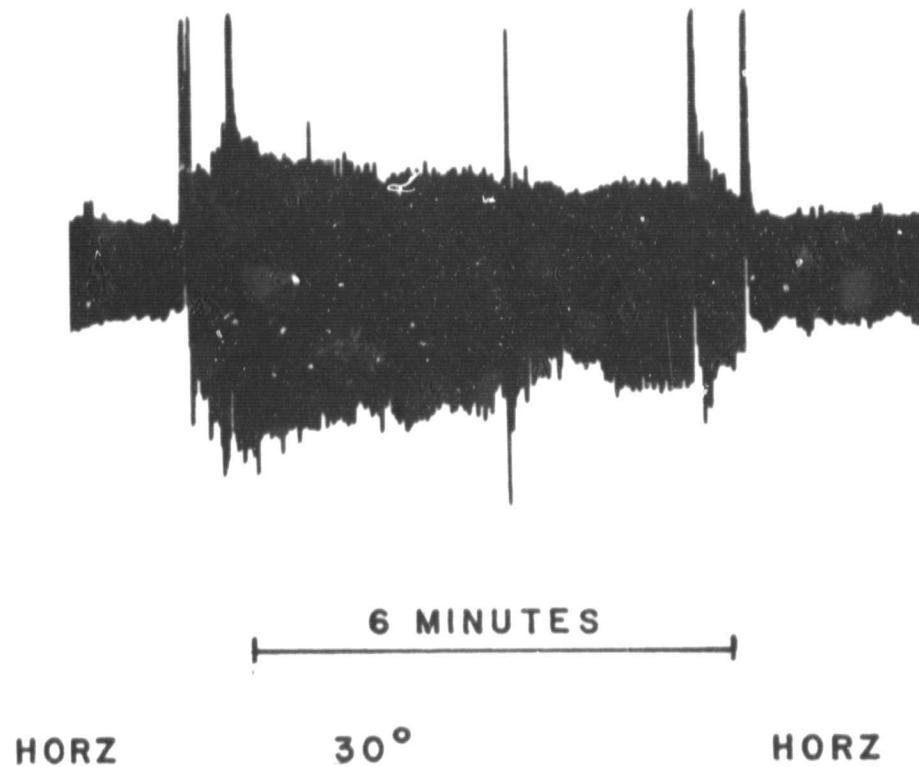


Fig. 9 Amplitude change in the spider heartpulse in response to a tilt of 30 degrees. The chart recording in this photograph was done at a very slow speed in order to expose the amplitude changes before, during and following a tilt of the animal. The sequence of events shows : a segment of the pulse before tilt, an electrical artefact indicating the beginning of movement of the tilt table, a second artefact showing the end of movement(when the table had reached 30 degrees), a segment of about 6 minutes at 30 degrees, and the artefacts associated with movement back to the horizontal.

During the tilt movement the amplitude increases to a large magnitude which slowly declines over a 6 minute hold at 30 degrees. During the return movement the pulse amplitude rapidly declines to the pre-tilt magnitude. An examination of the tilt response will be undertaken during the 1982-83 period. An hypothesis is that in order to compensate for the tilt of its body hydrostatic pressure is increased in the cephalothorax. The lyriform organs are differentially compressed and information is transmitted to the cardiac center supporting the cardiac reflex and serum enters the legs. This can be viewed, analogically, like a set of "lifts" which operate in a syringe-like manner to support the animal as the gravity vector is changed.

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Appendix A

The Centrifuge

The centrifuge employed in this research was constructed to insure: 1. the precise control of the speed of rotation, 2. the ability to manipulate the rise and decay of the rotational period and 3. with minimum of sound and vibration.

Figure 10 represents the essential features of the centrifuge and Figure 11 is a photograph of the centrifuge and ancillary apparatus.

Smooth acceleration and deceleration is accomplished by means of a ball and disc drive. We decided to use this technique for speed control in order to avoid the expense and difficulty of controlling an electric motor. The disc is rotated at a constant speed by a heavy duty, continuous motor. A stainless steel ball is supported by four ball bearings and can be positioned along the rotating disc by a screw arrangement. When the ball is centered on the disc no motion is transmitted to the output shaft. The variable output is transmitted to the centrifuge turntable through a speed reducer and a right angle gear drive. Since the speed of the electric motor is held constant the centrifuge period is linearly related to the position of the ball on the disc. The system does not require a feedback stabilized electric motor. Further there is a minimum of over- and under-shoot as a desired rotational speed is approached.

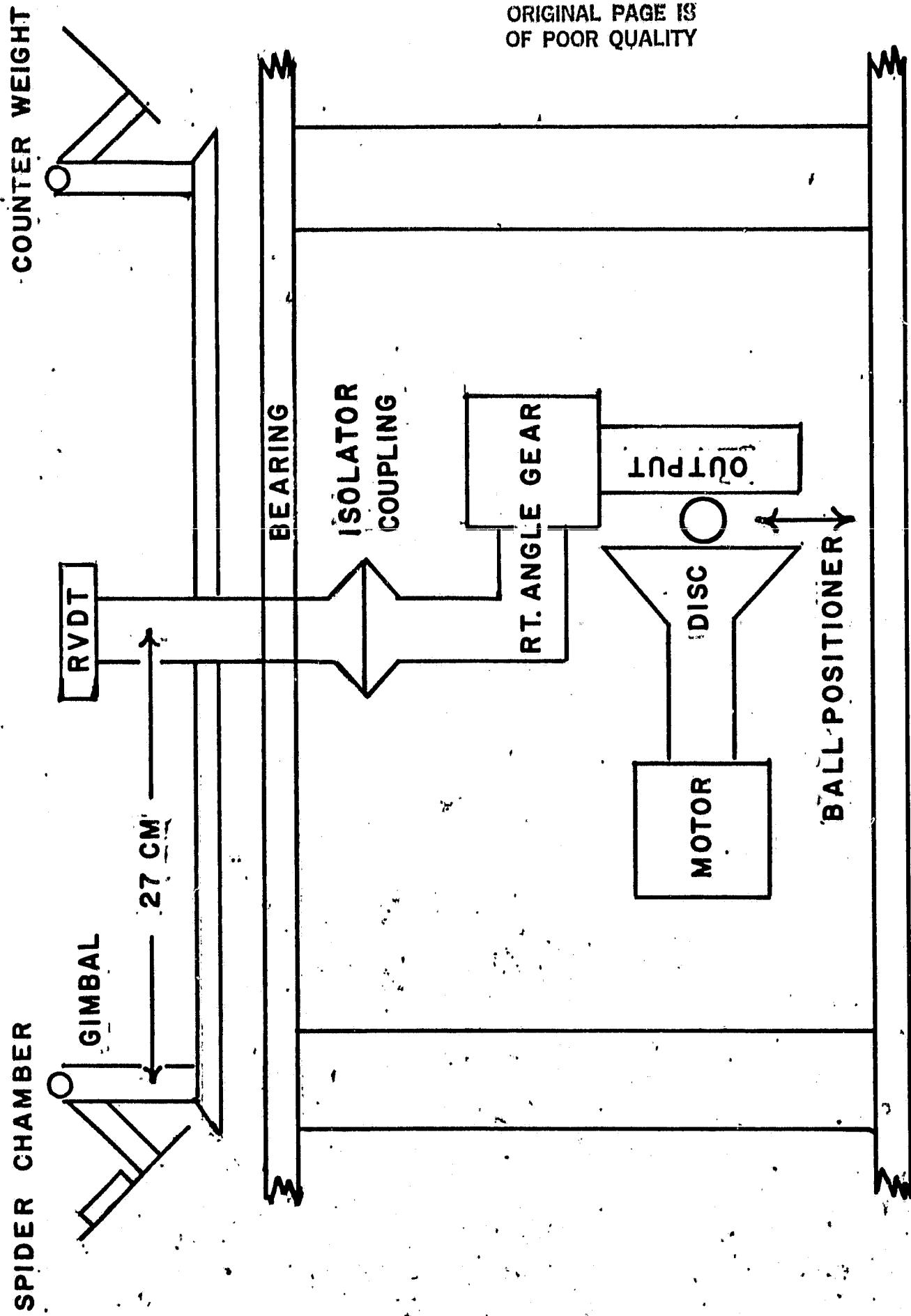
Figure 12 shows the deviation of the ball from the disc center (in millimeters) in order to achieve a particular centrifuge speed (in rev per sec). Each point in the figure represents the velocity needed to achieve an indicated G intensity. The position of the ball is typically changed by a small DC motor. It can also be varied manually.

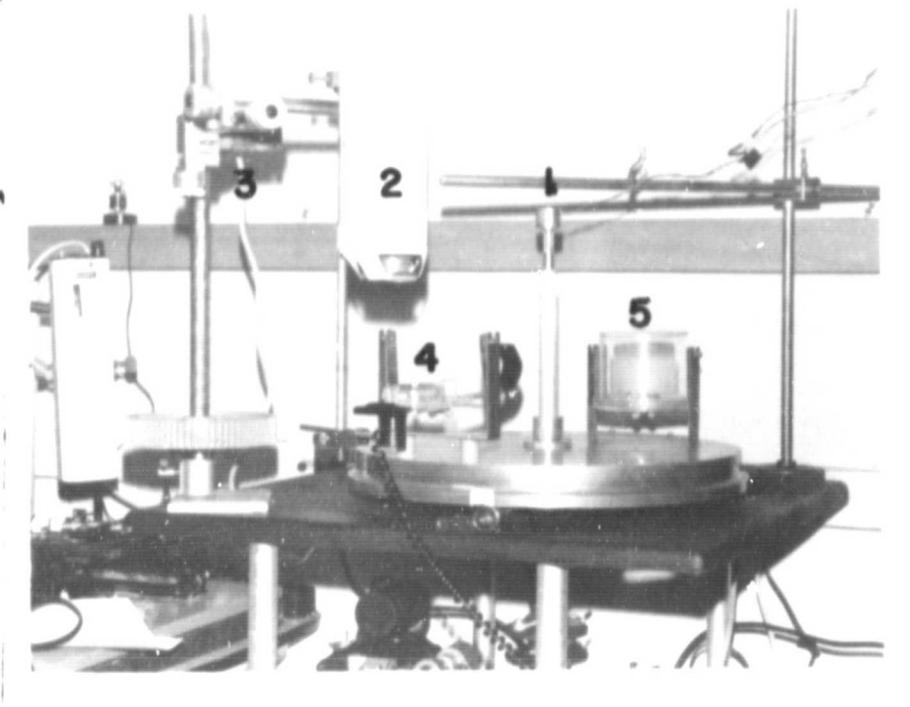
The centrifuge has excellent stability. Upon advancing the ball to a

desired position the turntable achieves a stable period within one or two revolutions. We measure centrifuge speed to the nearest millisecond. This is accomplished by a RVDT (rotary variable differential transformer) located at the turntable center. The RVDT voltage is delivered to an electronic counter which is triggered once per revolution. The velocity stability of the centrifuge is demonstrated in Figure 13 page 35. The ordinate is the period in msec for each revolution. The abscissa is successive rotations. The upper plot shows the results of 206 revolutions of the centrifuge set to 4425 msec/revolution. The lower curve shows 171 successive revolutions at a period of 2575 msec. Measurement sensitivity was +20 msec.

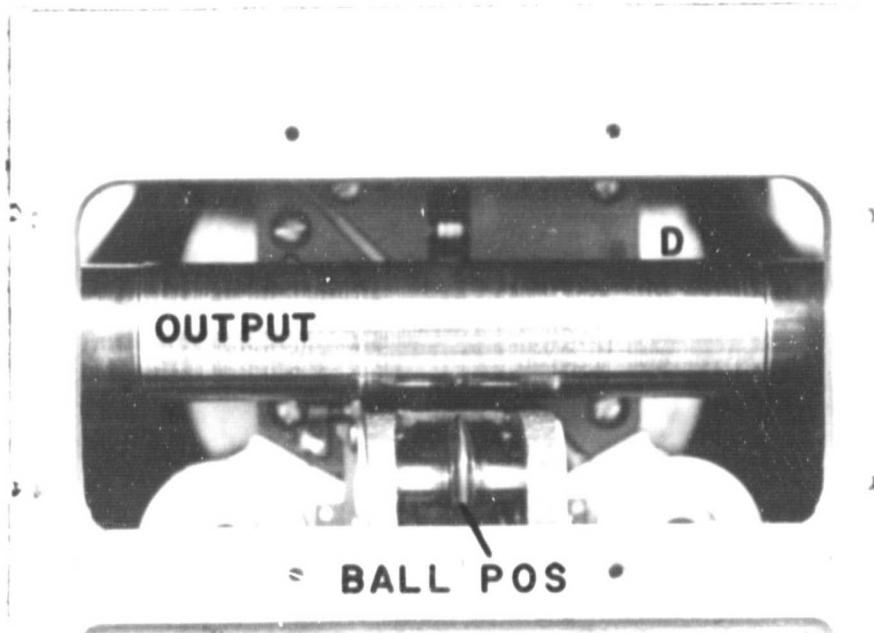
DIAGRAM OF THE CENTRIFUGE AND DRIVE SYSTEM

Fig 10.





A. CENTRIFUGE AND LASER (SEE TEXT)



B. BALL AND DISC DRIVE

Fig. II

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BLACK AND WHITE PHOTOGRAPH

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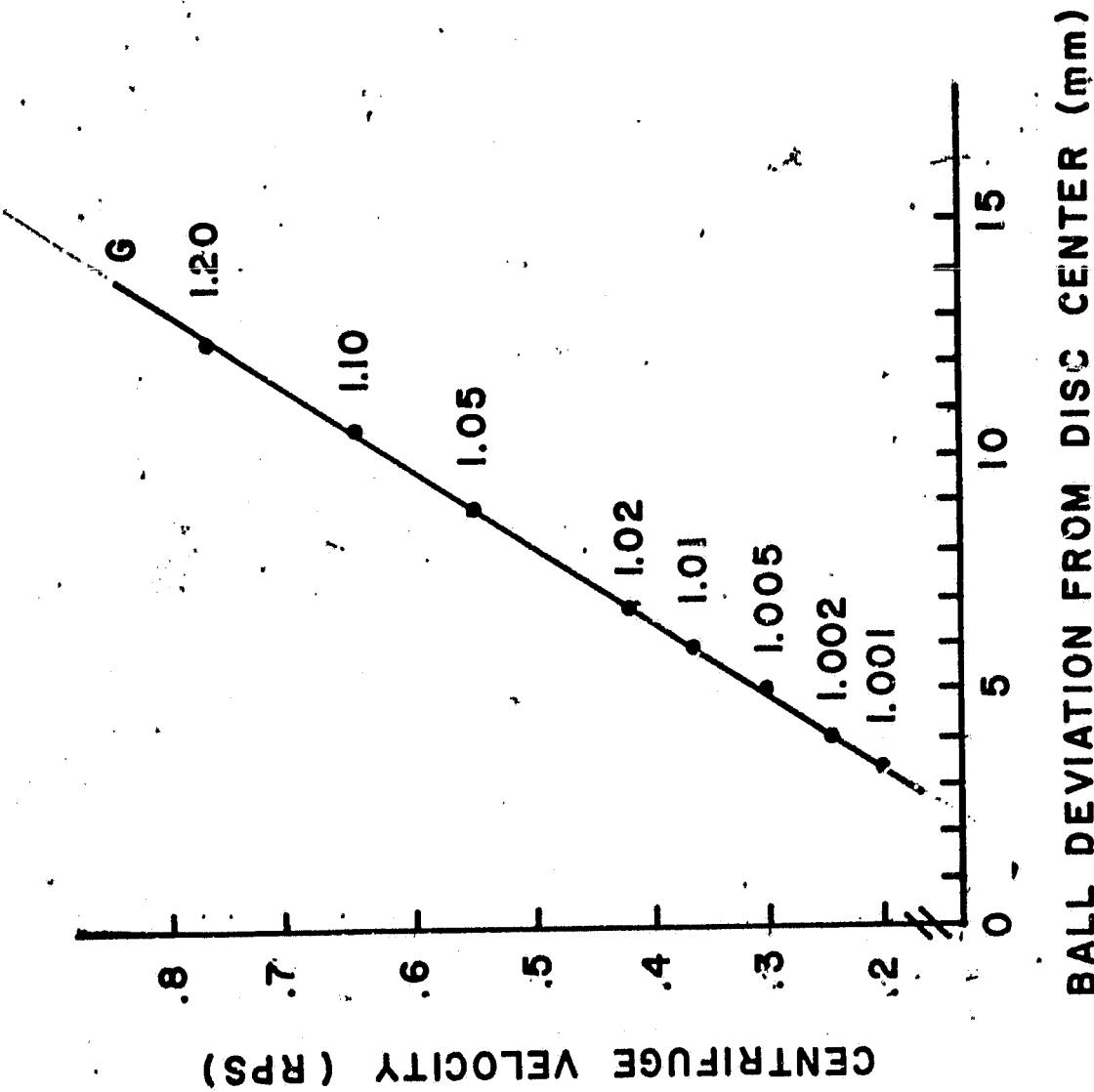


Fig. 12

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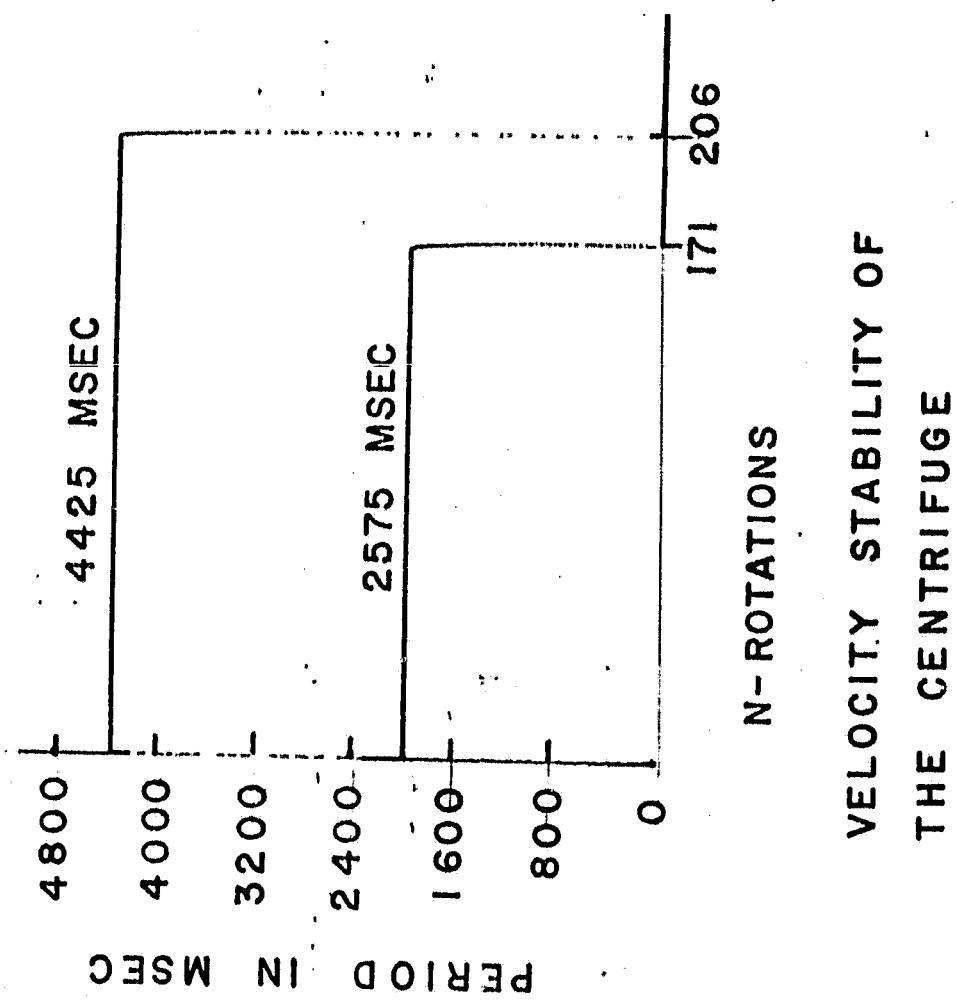


Fig. 13

VELOCITY STABILITY OF
THE CENTRIFUGE

Appendix **B**

A description of the System

Figure **14** is a schematic diagram of the system employed for the study of the spider heartrate as a function of Gz.

A laser beam (0.5 mW Metrologic) transilluminates the abdomen and heart of the spider. A photocell (PC) sensitive to 633 nm (the wavelength of the laser beam) receives light which has been modulated by movements of the heart or the fluid in it. These changes in light intensity are delivered to an amplifier (a Metrologic power meter) which has a DC output proportional to the light intensity change. The ouput voltage is delivered to a magnetic tape recorder (FM, Ampex FR 100) and to a Nicolet Instrument Computer.

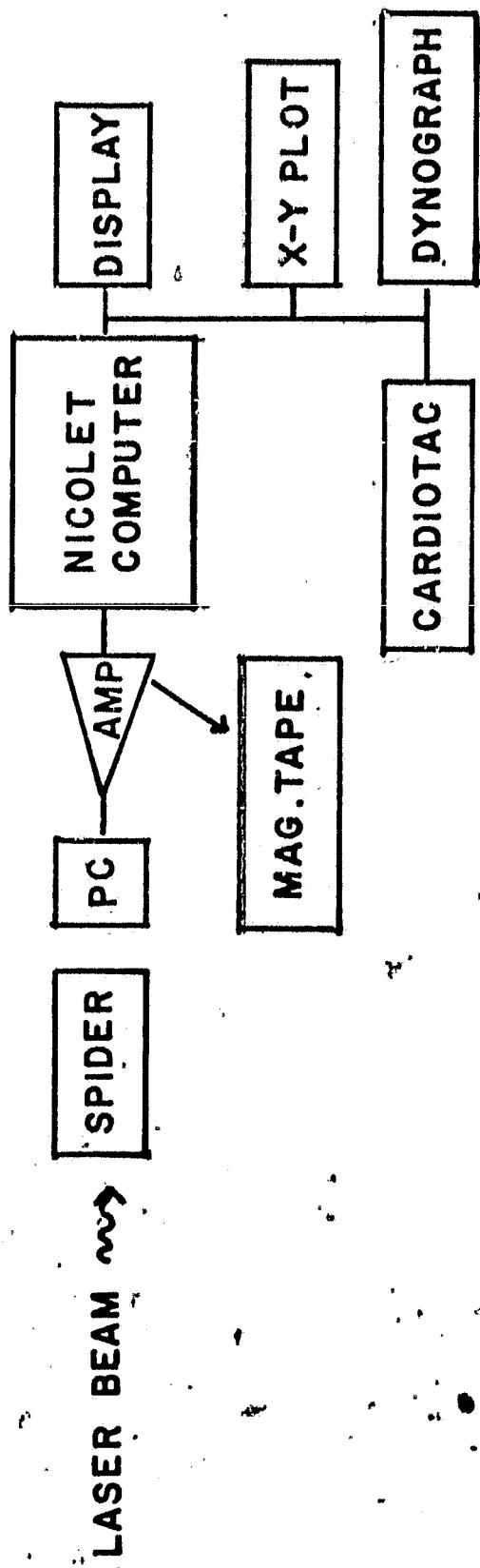
Other channels on the tape recorder record the output of a rotary variable differential transformer (RVDT) which indicates the period of rotation, a digital clock and a voice channel. The output of the Nicolet Computer is a time interval histogram (explained in section **G** page **46**). The display may be photographed or the histogram "read-out" on a X/Y Plotter. The "raw" data, i.e., the heart pulses are delivered to a 4 channel Dynograph Recorder (Beckman). One Dynograph channel displays an on-line cardiotac. The cardiotac allows the experimenter to examine the change in heartrate is "on-line". This instrument is a modification of a Nuclear Data 600 multichannel Analyzer. It is very useful for it suggests to the observer analyses which might be profitable at a later date. The Dynograph also records time hacks from the digital clock system (Datametrics Inc.)

Our Ampex FR100 tape deck is quite old and the 1/2 inch tape very expensive. We are now beginning to employ a Sony stereo tape deck with one channel of FM (Vetter Co.) and the clock information in the second channel. The

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system, although a bit ponderous, works quite well. In the coming year we shall begin to use an Apple II+ computer and ISAAC. ISAAC is a computerized data acquisition system with a special "Labsoft" language. The present tedious analysis of the data will be reduced and we shall have the capability of examining other aspects of the cardiac response now recorded on some 12 miles of tape.

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SCHEMA FOR THE RECORDING AND ANALYSIS
OF THE SPIDER HEART PULSE

Fig. 14

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Appendix C

Laser Characteristics

The laser (Metrologic Inc.) like any high-intensity light source produces heat. The instrument we employ yields a concentrated light beam of approximately 1 mm diameter at the locus of the animal. The wavelength is 633 nm. Temperature measurements indicated that the spot of light may add an increment of about 0.5 degree F relative to the ambient temperature of the laboratory. This is a low power instrument rated at 0.5 nW. In order to reduce the light intensity and minimize the temperature increase, the light was reduced by placing a heat protective glass (from a slide projector) in front of the laser's exit port. This procedure reduced the temperature increment to 0.3 deg. F when measured in an ambient temperature of 75 deg. F. Later we took measurements (Tektronix temperature sensor) with the heat filter in place and through the plastic culture dish in which the spider remains during and after rotation. The temperature increment was then reduced 0.1 deg yielding a total of about 0.2 deg. F. We do not feel that this is a very important extraneous stimulus to the animals cardiac response. We have recorded beats with the continued application of the laser light for 2 or more hours. There seems to be no tendency for a systematic change in the heartrate. If the laser illumination is pulsed (10 sec on - 10 sec off) we can observe no evidence for rate changes synchronous with the flash period. Our procedure avoids aiming the laser light on any of the eight eyes. Usually, spiders seem not to respond to visual exposure by laser. Spiders of our species are probably rather insensitive to laser light at the intensity and wavelength of our instrument.

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Appendix D

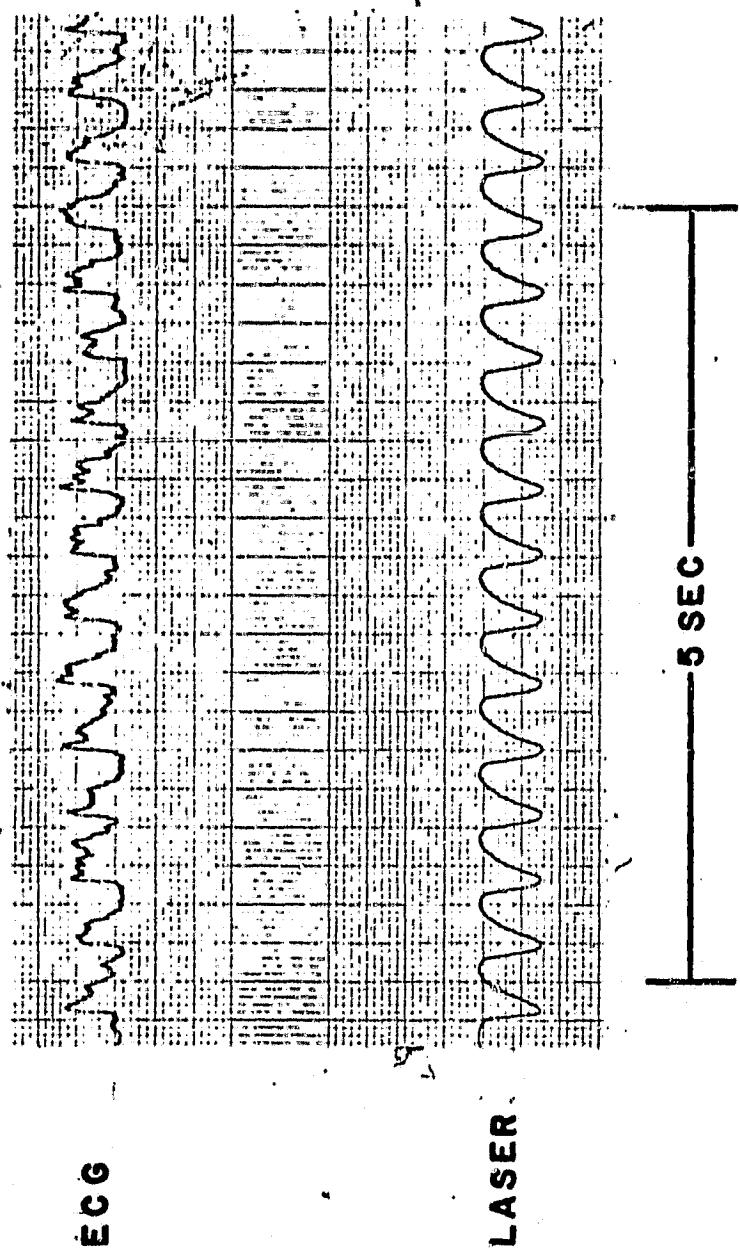
Corellation of the Electrocardiogram (ECG) and laser plethysmograph recordings of the heartpulse of the spider.

The invention of the laser plethysmograph was necessary in order to obviate the unphysiological high rates produced by the heart of a restrained animal. It is important to demonstrate that the laser approach provides a response comparable to the ECG in the study of the spider heartrate.

Figure 15 is a sample of a spider ECG and a simultaneous record of the heart pulse taken by laser. The animal is restrained.

The recording electrode was located along the midline of the abdomen just above the cardiac tube. The electrical response most probably derives from the activity of the dorsal-cardiac nerve which extends along the hearttube. The laser illuminated a nearby locus. The electrical and optical procedures are independent measures of the heart response. We cannot, at present, be certain what mechanism(s) produce the change in optical density. It could be a change in fluid density as it squirts through the heart, or perhaps, minute movements of the heart itself. Over a 5 second period one can count 12 beats. This is equivalent to 144 BPM an inordinately high rate relative to resting rates which are typically between 15 and 40 BPM. The high rate obtains when an animal is restrained (for purposes of ECG) and an electrode is touching the abdomen. Clearly, the need for a non-intrusive method is important. This exercise allowed the experimenter to judge that the laser method was sufficient for the purposes of the experiment.

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CARDIAC ACTIVITY RECORDED BY ECG AND
LASER FROM A RESTRAINED SPIDER

Fig 15

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Appendix E

Statistical Calculations

CHI Square in Testing the Hypothesis that the Distribution of Spider Heartrates is Gaussian.

The Gaussian, or normal probability distribution, has known characteristics and it allows the investigator to employ several powerful tools, especially on the judgement of the reliability of the data.

We have, in the present report, made no assumptions about the normality of the heartrate distributions (although they do "appear" bell-like). One reason for this is that the calculation of mean and variance from frequency data is quite tedious without computational aids. In a normal distribution, the mean and the median are identical. Our results are given in terms of the median. The method for determining the median is given in appendix H page 47.

A customary way of determining whether the discrepancies between theoretical (Gaussian) and obtained (empirical) frequencies are so large as not to be attributed to sampling errors is to employ the chi-square test. This test, as applied to the normal curve hypothesis, enables us to arrive at a decision as to the probability that an obtained set of frequencies (i.e., in the heartrate histogram) is not normally distributed.

The chi square test for normality was applied to the inter-beat interval distribution of several animals by determining the expected frequencies (based on the mean and variance of the normal distribution and comparing these to the obtained frequencies in the actual histogram. Chi-square, in all cases was not significant at the 0.05 level of confidence. Therefore we can conclude that the population from which the heart interval histograms arise is normally distributed on the measurement scale. Thus we are given the incentive and the

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logical right to employ parametric statistics in future data analysis. This will be accomplished by computer. Figure 16 is a plot of the obtained versus the theoretical distribution for one animal. It was calculated and plotted by hand (a tedious exercise). The obtained distribution is not significantly different from the Gaussian distribution of expected frequencies of occurrence of heartbeats.

chi square (χ^2)

$$\chi^2 = \sum \frac{(f_o - f_e)^2}{f_e} \quad df = N - 3$$

$$f_e = \frac{iN}{\sigma} y$$

Where f_o = observed frequencies of the heartbeat

f_e = expected frequencies based on the Gaussian distribution

n = number of observation

i = size of class interval

j = standard deviation of the obtained (measured) distribution

y = the ordinate of the Gaussian distribution for a particular standard score (z)

$$z = \frac{x - \bar{x}}{\sigma}$$

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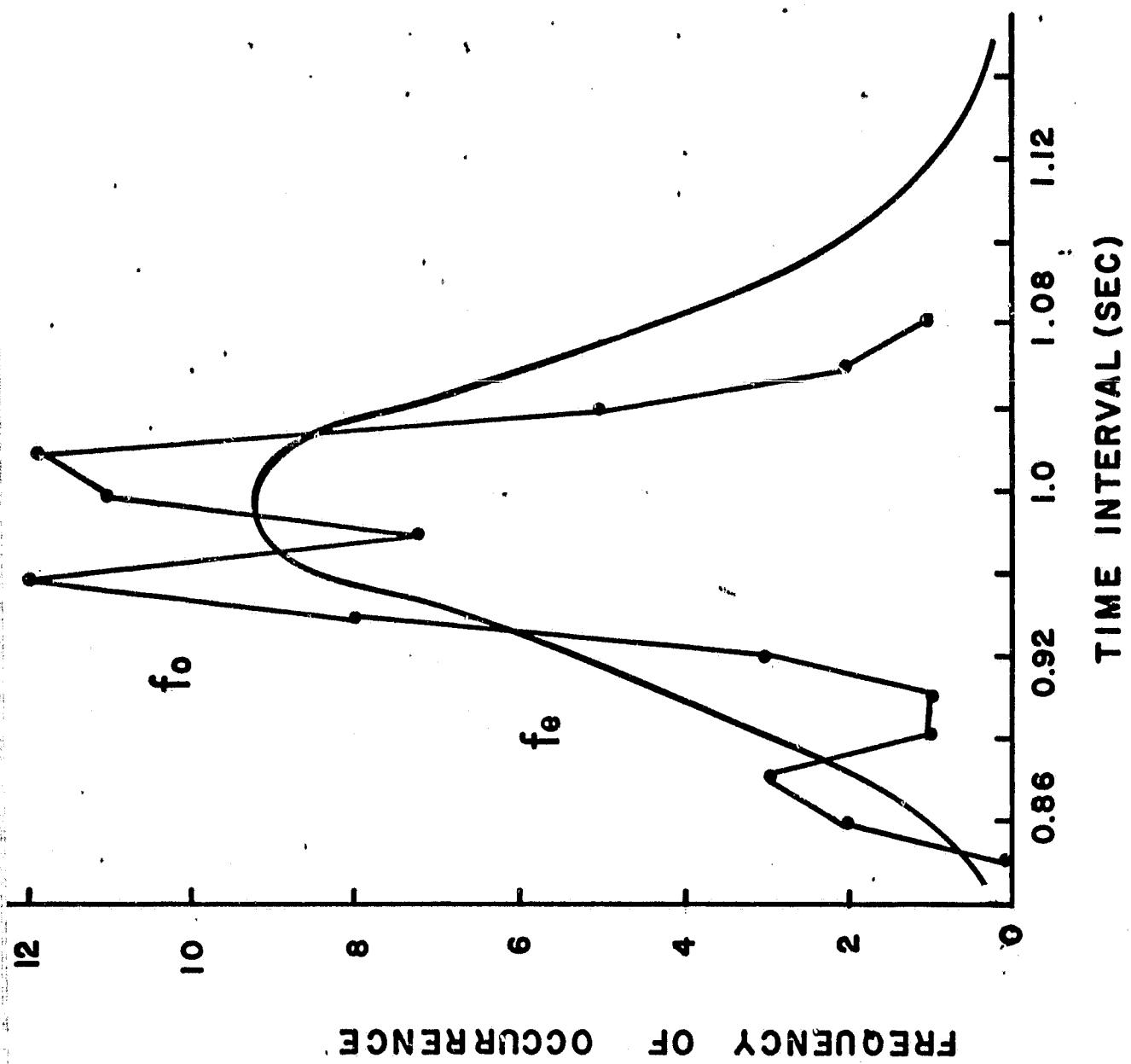


Fig. 16

Appendix F

The Spider Chamber Characteristics on the Centrifuge

The spider chamber (labelled 4 in Figure II A) is on a gimbal. The center of the chamber is 27 cm from the "dead center" of the centrifuge hub. This chamber is an enclosed tissue culture dish 5 cm in diameter. The animal is always located between 27 and 28 cm from the hub center. The specificity of Gz is therefore calculated between 27 and 28 cm. Because we do not wish to manipulate the spider when she's placed on the centrifuge 1 cm represents the Gz error. For slow centrifuge speeds (e.g. period of 4.93 sec) if the spider's locus is 28 cm, Gz will have increased from 1.0009 to 1.0010, an increment of 0.0009 percent. If at a high speed (1.28 sec) the animal is located at 28 cm the G increment is from 1.200 (27 cm) to 1.213 (28 cm), a change of 1.08 percent. These are the worst cases. Our estimation is that G can be specified between .009 and .5 percent at low and at higher rotational speeds. The tissue culture dish is a wind screen and it is counterbalanced for the "resting" position.

Figure II A also shows a second chamber on a gimbal. This is the early chamber for taking recordings from restrained animals. It now serves the role of a counter weight (labelled 5) 1, shows the RVDT. 2, is the laser which can be "swung" over the spider chamber and adjusted by 3, a micro-manipulator. The laser/manipulator is weighted with a heavy gear and the entire unit rests on anti-vibration mounts.

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APPENDIX G

The Time Interval Distribution (HIST, interval histogram)

The first pulse of a train of pulses starts the time measurement process and the next succeeding pulse both stops that measurement and simultaneously (within 10 microseconds) starts the next one. As each time interval is digitized, one count is added to a memory address whose number is proportional to the measured time interval. The time resolution in our experiments are typically 50 msec or less (20 msec for an animal presenting a more rapid beat). After 100 intervals are measured the time scaling procedure automatically stops. A "window" adjustment allows the experimenter to set a level such that only beats which exceed possible base-line noise are counted.

Appendix H

Calculation of the Median Heartrate from the Interval Histogram.

Figure 17 shows an interval histogram (IHST) which might obtain for a very large number of spider heartbeats. The time interval between each successive beat is on the abscissa and the frequency of occurrence on the ordinate. When this distribution is integrated it forms a cumulative frequency curve. When N is known it is a simple matter to locate the median (the 50th centile) directly or to interpolate between two adjacent time intervals.

The interpolation formulae is:

$$\text{median} = L + \frac{0.5N - f_b}{f_b} i.$$

Where: L = lower limit of class interval containing the median

f_b = sum of all frequencies below L

f_p = frequency of interval containing the median

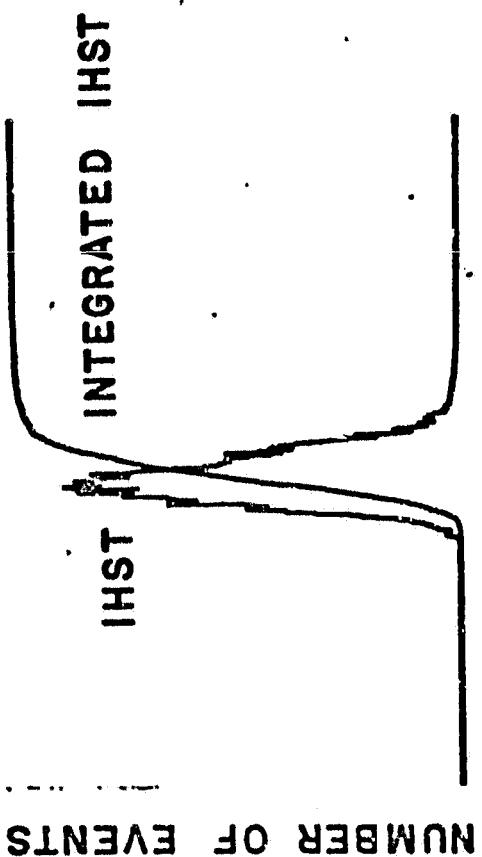
i = size of the interval

N = number of observations

The time interval histogram is integrated by replacing the number in each time interval address by the sum of the contents of all previous addresses, plus its own contents. The mathematical operation is:

$$x_i = 2^{-N} \sum_0^i x_i = 2^{-N} (x_0 x_1 + \dots x_i)$$

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?Fig.17

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APPENDIX I

Calculations for the force produced by radial acceleration on a typical 100 mg spider near the threshold of G_z sensitivity.

Given: $\ddot{a}_n = 0.4 \text{ m/s}^2$ $\ddot{a}_n = \text{Radial Acc.}$

$$\begin{aligned} g_t &= \sqrt{(0.4)^2 + (9.80655)^2} \\ &= 9.814804 \quad (\text{total } g) \end{aligned}$$

$$\begin{aligned} G_z &= \frac{9.814804}{9.80655} \\ &= 1.0008 \end{aligned}$$

The AVERAGE weight of a typical female SPIDER, A. sericatus is 100mg.

$$\begin{aligned} F \text{ in newtons} &= 1 \times 10^{-4} \text{ kg} \times 0.4 \\ &= 4 \times 10^{-5} \text{ N} \\ &= 40 \gamma \text{ N} \end{aligned}$$

FOR $G_z = 1.001$ (NEAR the Absolute threshold in our work).

$$\begin{aligned} \ddot{a}_n &= 0.93 \text{ m/s}^2 \\ F &= 1 \times 10^{-4} \times 0.93 \\ &= 43 \gamma \text{ N} \end{aligned}$$

IF Bohnenberger's (BARTH) measurements apply to our work the force on a very small spider, e.g. 50mg, at $G_z = 1.001$ would be ineffective in producing a CARDIAC RESPONSE.

$$\begin{aligned} F &= 5 \times 10^{-5} \text{ kg} \times 0.43 \\ &= 21.5 \gamma \text{ N} \end{aligned}$$

APPENDIX J

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Calculation of total gravito-inertial force.

G_z is the ratio of g_t/g_e

Where $g_e = 980.665 \text{ cm/sec}^2$ and $g_t =$ the vector sum of angular acceleration and g_e .

Computational formulae

$$\omega_r = \omega^2 r = \left(\frac{1}{\text{Period}} - 2\pi \right)^2 r$$

$$g_t = \sqrt{\omega_r^2 + g_e^2}$$

$$G_z = g_t/g_e$$

The general reference is Sears, F. W. and Zemansky, M. W. College Physics, 3rd Edition, Addison-Wesley, London.

The computational formulae have been programmed into a small desk calculator (T159). A printed read-out indicates TIM (period in secs) RPS, velocity, acceleration, total G and G_z ("g"). The program is extremely useful for calculating G_z when rotation periods other than the fixed ones of the present experiment are employed. An example of a "print-out" is attached below.

27.

1.28	TIM
131.5359401	VEL
650.5773926	ACC
1176.84102	GT
1.200043868	"G"

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Abstract

Orb weaving spiders depend primarily on mechanical stimuli for contact with the environment. Arachnids alone contain a specialized organ on the legs which convey information about cuticular deformation and vibration to the nervous system. Research has shown that these organs, the lyriform organs, and the legs themselves make up a complex sensory system. The system includes a control feature which may permit the spider to regulate its own sensory input. Spiders do not contain anatomically specific gravity receptors. The known anatomy and physiology of the lyriforms recommend them as a source of gravity information. The neurogenic heart of the spider has been shown to respond to a variety of sense stimuli which produce changes in the rate and possibly the vigor of the heartbeat. This research examines the effects gravito-inertial forces and variations in the leg/lyriform system have on the heartbeat of the spider. The experiment is designed to inform us about the gravito-inertial sensitivity and its possible mechanism in this ubiquitous and ecologically important animal.

Gravity receptors among the invertebrates are extraordinarily diversified. Some invertebrates have evolved special mechanisms for the detection and processing of gravito-inertial stimuli, however, it is generally recognized that many invertebrates do not present an anatomically distinct gravireceptor. Observations that these animals respond behaviorally to gravito-inertial forces ('g' in the remainder of this application) implies that structures like cuticular hairs, campaniform sensilla or endogenous receptors are involved in 'g' sensitivity (Bullock and Horridge 1965, Markl 1974). Among the arthropods, spiders represent a "case-in-point" for this issue. In this proposal we review the relevant spider literature, present evidence for 'g' sensitivity in the spider and propose an experiment for evaluating hypotheses on the mechanism for 'g' transduction and the spider's sensitivity to varied 'g' force.

Gravity, as a stimulus is, in some ways the easiest to study. All animals are influenced by it, except perhaps those in perfect equilibrium with water, and these usually have an eccentric center of gravity which causes them to assume some species-specific orientation. In some ways the study of gravity as a stimulus is most frustrating due to its general uniformity on the surface of Earth. In order to study 'g' one must control it and modify it. The modification of 'g' easily available in the laboratory is with the aid of a centrifuge or by impact (acceleration-deceleration). Outside the laboratory 'free-fall' is a most desirable stimulus condition. The laboratory centrifuge method permits the experimenter precise control over the magnitude and direction activities which expose the 'hidden laws,' the functional relationships between stimulus and response.

Spider Gravity Reception in the Literature

Studies which attack gravit perception among the spiders are virtually non-existent. Markl (1974) reviewed the invertebrate literature in which more than 270 studies were cited. He reported only two, older researches (1930's) which suggested that arachnids might employ 'g' for finding their way in the webs. According to Markl, "... nothing is known about the receptors involved (pg. 39)." A literature search to the present adds little to this meager history.

A consequence of a variation in 'g' is a variation in mass. There exist two studies in the literature in which mass was added to the spider body in order to evaluate web construction behavior. Mayar (1953) observed that orb-webs constructed by weighted spiders were simpler and showed an eccentric inner spiral. She felt that this eccentricity might be due to a gravity effect. Christiansen, Baum and Witt (1962) added a 30 percent increment to the weight of orb-weavers. They found a statistically significant decrease in total thread length in the webs of weighted animals which length returned to the pre-weighted, control lengths about 3 days after the weights were removed. These researchers also observed a doubling of the thickness of the silk (measured by protein analysis) in response to the 30 percent addition. Silk thickness also returned to control values 3 days after removal. Thus, a heavier spider builds a thicker thread for support and it is smaller because of the limited amount of protein available.

The "Sky Lab" flight of 1973 included orb-weaving spiders. The only report I could locate on this (NASA 1977) indicated that spiders could construct a web under conditions of free-fall. Unfortunately an analysis was not made of web geometry relative to the earth-bound orb. The writers of this report also indicate that the silk was "significantly finer (in flight)" compared to pre-flight controls (pg. 47). The method for determining thickness is not given. This could have been predicted from the 'added-mass' studies described above.

Other Evidence for 'g' sensitivity among orb-weavers

That spiders respond to 'g' come from 'field observations' and preliminary studies in the Neuro-Sensory Laboratory, Temple University.

In the field or in the laboratory, orb-weavers assume a head-down orientation in the hub of the web. Fig. 1, page 21 is a photograph of a spider in her web. When the frame which contains a web is totated 180 degrees the animal will, after some initial disorientation, rotate her body 180 degrees to return to the head-down position. This orientation response can also be observed with animals maintained in Petri dishes in the lab. A favored resting orientation in the dish is ventral-up. If the dish is gently inverted most animals return to the ventral orientation over a period of many minutes. Curiously an active spider (usually dorsal-up in the Petri dish) when inverted re-orient with a very short latency (possibly milliseconds). These behaviors indicate geo-orientation, and with a response reaction time which might depend upon the "state" (neuro-pharmacologic) of the animal.

The geometry of the orb-web also appears to express a gravitational influence. Examination of the lower part of the web (page 21) shows that the radial fibers are 'laid down' with smaller angles than the upper radials. This would imply that the lower part is stiffer than the upper part. Therefore, sag, due to the total web mass (silk plus spider) might be controlled. It is reasonable to believe that the differential placement of radial silk in the orb informs us as to the direction in which the spider "perceives" the 'g' vector.

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Heart Rate of the Spider

Physiologists and psychologists often employ heart rate as a dependent variable in the evaluation of sensory, emotional and cognitive stimuli. When used among the vertebrates this method for studying the senses has a limitation in that the myogenic (muscle) pacemaker in the heart and the autonomies to the heart act is to maintain a relatively constant rate. Thus the "orienting response" to sensory stimuli is usually observed as a momentary bradycardia (slowing down of the heart rate) following the onset of the stimulus. The spider pacemaker is different from that of vertebrates. Its heartbeat, is controlled by a direct neural mechanism. Hence the term neurogenic heart. The immediate stimulus for the beat arises in the dorsal cardiac nerve (first reported by Wilson 1967). The central reference for the cardiac pacemaker must be in the nervous system of the spider, however, to the best of my knowledge, there are as yet reports in the literature on the representation of the nerve in the central nervous system. There exists a small but growing literature on the physiology and anatomy of the spider heart. Several of these report changes in the rate of beating exogenous stimuli are accidentally or purposefully applied.

Simultaneous intracellular recordings from the cardiac nerve and mechanical recording of the beat permitted Bursey and Sherman (1970) to conclude that the beat and all subsequent activity depended upon the nerve pacemaker, and this functioned similarly to the cardiac ganglia of Limulus polyphemus and decapod Crustacea (other arthropods known to have neurogenic hearts). Sherman et al. (1969) examined 28 spider species histologically. They all presented a dorsal cardiac ganglion. Therefore, it is likely that the neurogenic heart is a basic characteristic of spiders.

Experimental situations in which spiders are restrained produce an increase in the basal heart rate (Wilson 1967, Sherman and Pax 1968, 1970). In order to determine basal (resting) rates for unrestrained spiders, Carrel and Heathcote (1976) transilluminated animals by Ne-Neon light. They reported resting rates from 9 to 125 beats per minute. Their results described a linear power regression between heartrate and spider body weight. Spiders are known to employ a hydraulic mechanism for the extension of the legs (Parry and Brown 1959), thus blood serves a mechanical as well as respiratory function in the spider. Carrel and Heathcote explained the transient bradycardia sometimes seen in an excited animal as a kind of "back pressure" arising from the increased pressure in the prosoma and abdomen (page 149). This could be an explanation for changes in heart rate associated with locomotor activity (struggling or jumping). In motor activity then, one would expect to observe the beat change caused by internal pressures (cardiac activity) followed by leg movements. During simultaneous recording of the heart beat and microscopic examination of the spider's legs I have seen movements of the leg lag beat change. However, when sensory stimuli are applied to the spider (minute tactile, thermal or vibration stimuli) and there is no perceptible movement of the spider under the highest visual amplification, a bradycardia can still be observed. In human beings this is sometimes referred to as a "bradycardia of attention" (Lacey and Lacey 1978). It is explained as a result of central mediated control by the vagus nerve among the vertebrates. Spider hearts do not appear to contain an equivalent parasympathetic control system therefore it is possible

that brady- and tachycardias not produced by leg movements are a consequence of sensory conduction to the CNS as well as spontaneous visceral activity.

The increased heart rate of restrained spiders does not seem to obviate the response of the heart to sense stimuli. Wilson (1967) observed that among restrained animals air currents, vibration, sound and in certain species light stimuli may all produce changes in the timing of the heartbeat.

Here, at Temple University, we have examined the feasibility of measuring 'g' effects according to the heartbeat of the restrained animal. The preliminary data show that for very small values of angular acceleration the beat slows down (bradycardia) and for increasingly higher acceleration the heart increases its frequency. Examples of cardiac histograms are given in Fig. 3, page 22.

In summary: observations have been offered to evidence that the behavior of the spider (orientation), her construction (the orb-web and the silk), and her physiology (cardiac response) all favor an organism which responds to gravito-inertial forces.

The Lyriform Organ: Its Possible Role in Spider Gravity Perception

Spiders have evolved a special receptor on their legs, the lyriform organ, to perceive deformations in the exoskeleton. The organs have been likened to Campaniform sensilla usually identified as having mechanical/proprioceptive functions (Bullock and Horridge 1965, Pringle 1955). Earlier observers had argued that the lyriform was a special chemo-receptor (McIndoo 1911, Kaston 1935) but the weight of recent experiments has obviated this belief.

A scanning electron micrograph of a lyriform complex is presented in Fig. 2, page 21. This organ is located on the patella of the second legs (as well as the first legs) of the orb-weaver *A. sericatus*. It presents a number of parallel openings in the exoskeleton; the overall configuration resembling a harp or marimba (hence lyriform). The larger organ in the photograph contains about 20 slits in a papilla, and these slits are lined-up with the long axis of the leg. A second organ containing about 18 slits, and at an angle of about 45 degrees is located distal to the larger one. Patellar lyriforms I have examined may contain as many as 15 to 35 slits. The longer slits may be about 100 microns and the shorter less than 3 microns in length. The trough of each slit is composed of fine filaments of cuticle and at one end an indentation locates the site of the dendrite of the sensory nerve. Walcott and Van Der Kloot (1959) observed, in electron microscope sections, each slit innervated by a single sensory nerve. Barth (1976) reported a peculiarity of the lyriform in that a second dendrite arises from the same sensory cell. The function of this second dendrite is unknown.

A less elaborate organ can be found on the tibia of the front legs. Compound organs have not been observed to this date in *A. sericatus* on the metatarsus. A compound organ can possibly be identified at the very tip of the tarsus on the first legs only and just below the 'comb'. The remainder of the tarsus and the femur appears to be devoid of lyriforms. (I am presently examining the spinning legs for the presence of lyriform organs.) In a comparison among arachnid orders Barth and Stagl (1976) observed a few single slits in the 'harvestman'

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at the proximal part of the leg (trochanter) and a greater frequency of occurrence of isolated slits in the 'whip scorpion'. Their 'hunting spider' (*Cupiennius salei*) was rich in lyriform organs. Perhaps sedentary animals, like orb-weavers, have fewer lyriform organs? If this is the case one of their functions might be to guide ambulatory behavior? Seyfarth and Barth (1972) demonstrated that the lyriform may be involved with kinesthetic orientation because when they were compromised in the hunting/walking spider the animal had difficulty in returning to an earlier spatial location.

Physiological and morphological studies strongly suggest that the lyriform organs transduce cuticular strain (Pringle 1955, Barth et al. 1975, 1976, 1978). The 'decisive' mechanical parameter appears to be a displacement of the slit. Compressional loads on the leg lead to some bending of the cuticle and this deformation at the site of the lyriform is the adequate stimulus. In one respect the lyriform shows a directional sensitivity in that dilatation of the slit does not elicit neural activity (Barth 1976).

The exquisite absolute displacement thresholds of the lyriform were first reported by Walcott and Van Der Kloot (1959). They estimated a threshold of 25 angstrom when 200 Hz vibrations were applied to the excised leg of the common house spider. This sensitivity was confirmed in later work by Walcott (1963, 1969). Finck (1972) employed average evoked potentials from the unanesthetized spider brain (the sub-oesophageal ganglion), in order to measure the absolute threshold among orb-weaving spiders. His results indicated values less than 100 angstrom when 90 Hz vibrations were applied to the tip of the tarsus. The differences may be due to the species examined and the experimental methodologies employed. Barth and Bohnenberger (1978) used ramp and hold displacements to evaluate the response of the lyriform organs in the 'hunting' spider. Their results were given in terms of degrees of metatarsal excursion. Individual slits were seen to respond to excursions as little as 0.01 degrees. Therefore, minute movements of the spider leg, whether produced by vibration or by constant (step) displacements are adequate stimuli for initiating responses in the lyriform organ.

Finck and Reed (1979) employed a reflex movement of the spider leg as a dependent variable in a study of sensitivity to substrate vibration. The latency of the reflex response was seen to be inversely related to stimulus intensity. A 1 micron (rms) substrate displacement could elicit a response with a reaction time of about 100 msec, whereas displacements on the order of 0.05 micron resulted in latencies of about \pm 1000 msec. Behavior thresholds were seen to be of the same order of sensitivity as the majority of single unit thresholds in the same species. The behavioral spectral sensitivity of the spider was also comparable to the "tuning" according to electrophysiological criteria. It is not surprising to find some differences between behavioral and physiological estimates of sense function. As we have indicated the application of the stimulus, whether direct to the leg or to the substrate and whether the subject is an excised leg or a live animal etc. offer us different views about sense function. In the physiological studies employing single neural unit responses individual units show a range of displacement sensitivities. Apropos of this an important but still unanswered question concerns the magnitude of the neural input to the brain needed to elicit motor behavior. It seems, from what has been reported on the spider, that the activity of very few neurons is sufficient to produce a behavioral response.

Lyriform organs rest on legs and are typically located laterally, near a joint. It is reasonable to believe that the leg of the spider be considered an important part of the conductive system for the lyriform and other mechanoreceptors on it. The results of several experiments indicate that the leg position is a variable in spider mechano-sensitivity. The characteristic posture of the spider in its web is cephalothorax down and legs extended. It is very possible that this represents an optimal positioning of receptors and accessory structures in order to enhance sensitivity to web movement. Walcott and Van Der Kloot (1959) reported that "tuning" of the lyriforms on the leg of the common house spider could be altered by changing the position of the leg. Finck (1980) was unable to confirm this result in an orb-spider but he did find that the absolute threshold could be raised or lowered by altering the position of the animal's leg. For example, a single neural unit had a characteristic frequency (its best tuning point) near 50 Hz and with a threshold of 0.004 micron when the leg was extended. When the leg was bent close to the cephalothorax the threshold was increased (sensitivity reduced) to 0.89 micron. This corresponds to a threshold displacement difference of 224:1, i.e., 47 dB. This dramatic sensitivity change was accompanied by very little frequency shift in tuning.

An explanation for this phenomenon is not yet forthcoming from the literature. As a 'working hypothesis' I propose that the role of the leg in this system is a lever in which the ratio of the work: effort arm changes according to leg position, i.e. the fulcrum location varies. We know, for example, that among the vertebrates weak airborne stimuli (sound) is substantially amplified by the middle ear mechanical system. The amplification contributed by the areal ratio of the tympanum to stapes footplate and the ossicular lever can deliver a stimulus increased by a factor of almost 100:1 (40dB). If we are willing to view the orb-web as an extension of the sense mechanism (as well as a snare) and the leg of the spider as a lever an interesting analogy is tendered. Perhaps spiders evolved a similar mechanical amplifier/attenuator, independently? In the "field" one can observe the spider vary her leg position. For example, a 100 Hz tuning fork applied near the animal may cause her to pull the legs tight into the cephalothorax. In this state the spider is remarkably insensitive to further stimulation (this response sometimes called "playing dead" may be likened to tonic immobility). If the tuning fork is applied some distance from the animal (at the web periphery for example) she will extend the front legs as if to optimize the reception of the vibrations. Thus the leg behavior of the spider functions like a variable attenuator which could increase or limit the mechanical input to the cuticular sense organs.

Bekesy (1967) described a variety of mechanisms evolved by organisms to attenuate unwanted information (noise) and enhance "needed" information. One simple method is to reduce the sensitivity of the receptor either directly (neural means) or through an auxiliary mechanism. Bekesy's examples are instructive in explaining the functional significance of adaptation and inhibition in sensory systems. For example, the anatomy of the olfactory apparatus of man assures, by aerodynamic means, that outside odors are favored over odors arising in the gut. In vision, the sensitivity of the human eye is sharply reduced in the infrared. Thus the abundant blood supply to the eye (body temperature circa 310 degree K) does not provide a continuing source of background radiation to the retinal elements. In animal behavior, the orienting reflex (startle, attentive behavior) also provides a mechanism for enhancing or avoiding sensory stimuli. In this large context, the possibility that the orb-spider can 'turn-on or turn-off' the mechanical sense system by merely re-positioning her legs is an exciting possibility for investigation.

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